

SAP-FEEDING AND ITS CONSEQUENCES FOR REPRODUCTIVE SUCCESS AND  
COMMUNICATION IN YELLOW-BELLIED SAPSUCKERS  
(SPHYRAPICUS VARIUS)

BY

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Herbivores that exploit sap have adaptations to overcome the defensive mechanisms of plants. Sap-eating animals face thick cuticles and clogging mechanisms that protect sap. Yellow-bellied sapsuckers (Sphyrapicus varius) exploit both the phloem and xylem sap of trees and are expected to have adaptations associated with this feeding habit.

Field observations from breeding seasons in 1991, 1992, and 1993 at the University of Michigan Biological Station near Pellston include 41 pairs of sapsuckers and their offspring. Hypotheses are tested about the mechanism of sap extraction and the consequences of sap feeding for reproductive success and drumming behavior.

Sapsuckers harvest xylem sap from trees for a brief period in early spring. Trees with higher concentrations of sucrose but not with higher sap flow rates are preferred. Sapsuckers extract phloem sap during most of the breeding season by making large square holes in the boles of trees. Phloem sap flows from these incisions, which is

surprising because incisions in sap tissue usually clog, preventing sap flow. Comparisons between trees used for sap extraction and those not used reveals that sapsuckers concentrate their efforts on individual trees. Observations show that sapsuckers repeatedly wound the tree above old wounds to form a cluster of sap holes, and may use saliva to unclog blocked phloem tissue. Experimental field manipulations demonstrate that sap feeding does not appear to influence reproductive success as much as the availability of nesting cavities. Sapsuckers use drumming as a form of acoustic communication, but they do not advertise the quality or quantity of sap trees with their drumming. Rather, field observations and manipulations reveal that they choose substrates for drumming that can give loud sounds of a low frequency when tapped.

Fewer specializations appear to be necessary to induce the flow of xylem sap than phloem sap from incisions through bark. Therefore, it is suggested that the exploitation of xylem sap may have been a precursor for the evolution of phloem-sap extraction. Many animals steal sap from extractors rather than extract it themselves and research on these animals may elucidate the evolutionary pathways leading to specialization on sap.

## GENERAL INTRODUCTION

Plants manufacture carbohydrates through photosynthesis. Animals exploit this resource from many parts of the plant, including green leaves, flowers, pollen, nectar, fruit, seeds, roots and storage tissues associated with roots. Specialization on specific plant parts often leads to the evolution of unusual adaptations in herbivores. The complex array of interactions that occur as herbivores obtain food and plants avoid being eaten has been, and remains, a central issue in ecology (see reviews in Courtney and Salabanks 1992, Bock and Linhart 1989, Bentley and Elias 1983, Futuyma and Slatkin 1983).

Plant sap contains carbohydrates and some animals have evolved ways of harvesting sap as food. Because sap is vital to a tree's survival and costs energy to produce, trees have evolved ways to protect their liquid transport systems from exploitation by animals. Trees have two types of sap, one contained in xylem tissues and one in phloem tissues. Xylem sap functions mainly in the transport of water and minerals from the soil to tissues in other parts of the tree (Salisbury and Ross 1992). As a result, during most of the growing season, xylem sap contains only trace amounts of sugars and amino acids. Only during a brief period in the spring does xylem sap have a slightly elevated sugar concentration as stored carbohydrates are mobilized and transported to newly growing shoots. In contrast, phloem sap serves in the transport of photosynthate from photosynthesizing tissue to growing or storage parts of the plant. It is relatively rich in carbohydrates and also has small amounts of amino acids (Crafts and Crisp 1971).

Animals that exploit either type of tree sap face several difficulties in exploiting this resource, including a layer of thick cuticle or bark that protects the sap-containing tissue, sap (usually xylem sap) that may be too dilute to be worth the effort (Haack and Slansky 1987),

and self-sealing properties of tree tissue that do not allow sap to flow freely from an incision (Kallarackal and Milburn 1983). Because of these barriers, a variety of unique adaptations is required to help animals obtain and use tree sap as a food resource (Raven 1983).

While the exploitation of tree sap results in the evolution of unique adaptations for harvesting sap, this feeding habit also has other consequences for sap eaters. Unlike some food resources from plants (e. g., flowers, fruit, and seeds) that are ephemeral or quickly depleted, sap provides a continuous source of food for long periods of time. In fact, sap availability may actually increase as more time and energy are expended to make incisions. For example, the territorial behavior of several species of primates centers around their trees used for sap and exudate feeding (Rylands 1985, Coimbra-Filho and Mittermeier 1978). Sap availability also influences the population density of sugar gliders (Petaurus breviceps) in temperate Australia (Smith 1982). In summary, a continuous supply of a resource such as sap clearly has consequences for territorial behavior and may also influence mating and other behavior.

Before describing tree sap and sap eaters in general, I want to contrast sap with tree exudates. Some trees produce exudates in their wood or bark that are different from the transport sap of the xylem and phloem. Sometimes these exudates are produced in the xylem or phloem tissue and can be confused with true sap. However, exudates, including resin, gum, kino, latex, amber, and balsam, are different from sap because they function not in transport but in injury response, especially preventing the spread of fungus infections from a wound (Hillis 1987). A variety of animals, including humans, exploit plant exudates either by mining what is naturally present or by adding additional wounds and bruises to induce exudate formation (Hillis 1987). While exudates offer an important food resource to some animals, the focus of my research has been the exploitation of the transport fluids of plants and not the plants' injury response system.

In this dissertation I examine the sap-feeding behavior of a species of woodpecker, the yellow-bellied sapsucker (*Sphyrapicus varius*). I begin with their xylem sap feeding habits (Chapter 1) and then explore different aspects of its phloem sap-feeding behavior with the next four chapters. The first chapter of the series on phloem feeding is a review of other organisms that eat phloem sap and speculation on the evolution of adaptations required for this specialized diet (Chapter 2). Other chapters in this group explore the mechanisms of how sapsuckers extraction phloem sap (Chapters 3-5). I also address some consequences of this sap-feeding habit, including how it may affect reproductive success (Chapter 6) and how it may influence drumming behavior (Chapter 7).

Yellow-bellied sapsuckers, which harvest tree sap throughout most of the year, are expected to have adaptations associated with their sap-eating habits. Sapsuckers wound trees by pecking holes through the bark to the cambium layer and then eat the sap that oozes from these holes. Sap makes up a major part of the diet for both adults and young (Beal 1911, McAttee 1911). Sap holes that the sapsuckers make can produce copious amounts of sap, and trees with several active holes often have wet trunks because sap overflows the holes and runs down the tree (Tate 1973). Considering that trees have self-sealing mechanisms to prevent sap from flowing freely from wounds, how are these birds inducing sap to flow from the holes that they make? As woodpeckers, they clearly have the ability to peck through the protective bark to the sap-containing tissues, but making holes is not enough to induce the flow of sap in most trees. The adaptations that sapsuckers possess for overcoming the self-sealing mechanisms of sap tissue have not been studied. In this dissertation I will address this general issue of how sapsuckers are able to harvest sap from trees. In addition I will present data on both xylem-sap and phloem-sap feeding in this species and discuss the implications of exploiting sap as a food resource.

The diet of yellow-bellied sapsuckers includes tree sap, fruit, and insects that are gleaned from tree trunks or caught on the wing (Tate 1973). Sapsuckers are unusual among woodpeckers because they do not excavate rotten wood for arthropods. Several authors

have suggested that sapsuckers also eat the phloem and cambium tissue, called bast, from the holes that they excavate because this material has been found in the stomachs of collected specimens (Beal 1911, Tate 1973).

Sapsuckers prefer nesting in living aspen trees (Populus sp.) that have been infected with heart-rot fungus (Fomes igniarius) (Kilham 1971). Pairs usually construct one new cavity each year, and the same tree, but not the same cavity, may be used for several years (Kilham 1977). As is typical for woodpeckers (Yom-Tov and Ar 1993), the eggs hatch quickly compared to other birds but the nestlings remain in the cavity for an extended period of up to 29 d (Jackson 1976). Both the male and female parent assist in raising young. Once the young have left the nest tree, neither the fledglings nor the parents return to the nest hole but they remain in the vicinity of the trees that they use for sap extraction (Lawrence 1967). Juveniles feed from their parents' sap holes for at least 2-3 weeks after leaving the nest (Foster and Tate 1966).

Yellow-bellied sapsuckers migrate in spring and fall between their wintering area in the southern U. S. and Mexico and their breeding grounds in the northern U.S. and Canada (Howell 1953). Pairs are clearly territorial during the breeding season but few interactions have been observed on the wintering grounds where individuals probably are not territorial. Throughout the year on migration routes, breeding grounds, and wintering areas, sapsuckers wound trees for sap (McAtee 1911). In the following chapters, I will focus on feeding habits during the breeding season, presenting data on both xylem-sap and phloem-sap feeding in this species and discussing the implications of exploiting sap as a food resource.

## CHAPTER 1:

### EXPLOITATION OF XYLEM SAP AS FOOD BY YELLOW-BELLIED SAPSUCKERS

#### Introduction

Yellow-bellied sapsuckers exploit both the phloem and xylem sap of trees. Their phloem-feeding habits are conspicuous and have been described by many researchers (Beal 1911, McAttee 1911, Kilham 1964, Foster and Tate 1966, Lawrence 1967, Tate 1973). Only a few have noted the possibility that sapsuckers may also take xylem sap during some times of the year (Lawrence 1967, Tate 1973). Even at its maximum sugar content, xylem sap is relatively dilute. So, it is not certain whether sapsuckers use xylem sap as a source of food or water. In this study, I report yellow-bellied sapsuckers harvesting xylem sap and I explore its possible use as food.

Xylem sap serves primarily to transport water and some minerals from the soil to the photosynthesizing parts of a tree (Salisbury and Ross 1992). The conducting elements of xylem tissue are tracheids and vessels. Both of these conducting elements contain no living protoplasm at functional maturity and are essentially dead, hollow tubes. Xylem sap moves up these long hollow tubes of dead tissue as a result of a water potential created by a combination of positive atmospheric and root pressure and a negative evapotranspiration pressure. Because the negative component of the water potential is the most important mover of xylem sap, incisions made into xylem tissue in the trunk of a tree usually do not exude much sap (Kramer and Kozolowski 1979). Only the outer layers of xylem tissue in an intact tree function in sap transport because the flow of sap eventually stops when inner, older xylem columns become clogged over time (Hillis 1987).

During most of the year, a tree's xylem sap is extremely dilute and contains only trace amounts of amino acids and minerals (Salisbury and Ross 1992). However, stored starch is mobilized as sucrose in the xylem at the beginning of the growing season. Carbohydrates that are stored in the vascular rays, which extend into the xylem tissue from the phloem, are transported via the xylem sap up to growing leaf buds in early spring (Gregory 1982). This higher-than-normal concentration of sucrose is coupled with extremely high positive pressures in the xylem sap that result from cold ( $<0^{\circ}\text{C}$ ) nights and warm, sunny days. Because of these seasonal fluctuations, xylem sap can be viewed by sap extractors as either a steady, low-quality food resource; an ephemeral source of higher-quality food; or a source, not of food, but of water.

Several kinds of insects including cercopids, cicadas and cicadellids exploit xylem sap as the main source of food for adults and nymphs (see Raven 1983 for review). These insects feed by penetrating individual xylem tracheids with their feeding stylets. Xylem-feeding insects encounter two problems: they must actively pump the dilute sap out of the xylem tissue because of the negative pressure, and they must void excess water that accumulates as they extract the small amounts of organic molecules available. Insects that make xylem sap their only food find it an energy-limited resource and are characterized by slow growth and long life cycles compared to close relatives that exploit other sources of food (Haack and Slansky 1987, Fitter and Hay 1987).

Several animals exploit xylem sap as only a temporary source of food. They extract xylem sap during the brief period when it has a relatively high sucrose concentration and flows freely from incisions. Heinrich (1992) found that in early spring red squirrels (Tamiasciurus hudsonicus) in Maine made incisions through the bark to the xylem tissue of sugar maple trees (Acer saccharum) and lapped up the evaporated sap below the wounds a few hours later. Heinrich concluded that these squirrels were not using the sap as a source of water because the squirrels had plenty of other water available and did not lap the dilute sap directly from the fresh incisions. Humans also take advantage of this spring xylem-sap



run in sugar maples and manufacture maple syrup and sugar from sap gathered from incisions in the trunk of trees (Walters and Yawney 1982). However, sap must be evaporated and the sugars concentrated by 22-43 times the original levels before the maple sap is considered valuable as food (Walters 1982). In both of these cases, the exploiters of xylem sap are able to obtain free-flowing sap by simple incision into xylem tissue because of the unusually high positive pressure. Although most of the year sapsuckers eat phloem sap from trees, sapsuckers also are able to exploit xylem sap for a brief period in early spring. In the following chapter I will explore how sapsuckers extract xylem sap. In addition, I will address the question of whether sapsuckers use this dilute xylem sap as a source of food or water.

### Methods

I observed yellow-bellied sapsuckers obtaining xylem sap 27 April through 9 May 1993. All observations were made at the University of Michigan's Biological Station in Cheboygan County. The habitat consisted of a mixed hardwood forest that had grown up after major logging operations in the early 1900's. Dominant tree species included sugar maple, red maple (*Acer rubrum*), aspen (*Populus* spp.), American beech (*Fagus grandifolia*), and white birch (*Betula papyrifera*). Sapsuckers are migratory and arrived in this area during the first week of April, before tree buds showed any hint of swelling.

Trees used for xylem-sap extraction were located by following birds on their foraging trips or by listening for the sound of sap dripping onto the dry leaves of the forest floor. Data were collected from trees on eight sapsucker breeding territories.

Xylem sap was collected from two kinds of incisions through the bark to the xylem tissue of trees: 1) holes that yellow-bellied sapsuckers made with their bills and 2) holes that I drilled with a small hand drill. I made the artificial holes with a sharp, 4.8 mm steel wood bit with which I cut through the bark and drilled approximately 4 mm into the xylem tissue of each tree at breast height. Sap flow rates were measured using a 1 ml tuberculin

syringe fitted with a needle. Each hole was completely evacuated and then after a timed interval, all the new sap that had collected in the hole was measured.

Fecal samples from wild birds were collected by spreading a 2 x 4 m thin sheet of plastic under a tree branch where a bird was feeding. The resulting fecal samples were collected and measured within five minutes of defecation. A captive juvenile was kept on a diet of dilute maple syrup and fecal samples were collected in the cage bottom on waxed paper. These samples were also measured immediately, within one minute of defecation.

Sugar concentration in sap and fecal samples was measured with an American Optical 10431 T/C Hand Refractometer with a range of 0-55° Brix. °B is a measure of the percent solute by weight, in this case grams sucrose per 100 grams water. Ambient temperature was measured in the shade within one meter of the ground.

A tree was defined as used by the sapsuckers for xylem-sap extraction if it had evidence of at least one bird-pecked hole with visible or audible sap dripping from a wound. Trees with no evidence of current yellow-bellied sapsucker activity were defined as unused for xylem-sap extraction. Tree size was measured as the circumference at breast height. I compared the sugar concentration and sap flow of sap from drill holes made at breast height in trees used for xylem-sap extraction and their closest neighboring tree of the same species and equal or greater circumference using a Wilcoxon matched-pairs signed-ranks test (Siegel 1959).

## Results

I observed yellow-bellied sapsuckers exploiting 21 different individual trees for xylem sap. Two of these were sugar maple and the other 19 were white birch. Xylem sap oozed from my incisions and bird peckings only on warm days during a short time in early spring before the beginning of leaf flush (9 days between 27 April and 9 May). Incisions made for xylem sap extraction by sapsuckers were approximately round with average dimensions of 4.0 ( $\pm 0.75$ ) mm x 4.8 ( $\pm 0.63$ ) mm (N=6). Unlike the typical pattern of vertical lines of

large holes made for phloem-sap extraction (see Chapter 4), xylem holes were made singly or in short horizontal rows of approximately 3 to 15 small holes. I found active holes on branches 3-6 m above the ground as well as on the main trunk of trees 0.05 to 11 m high (see also Tate 1973).

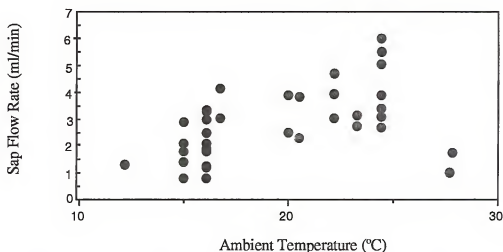


Figure 1-1. The flow rate of xylem sap in relation to ambient temperature.

All sapsuckers ingested fresh sap flowing directly from holes in the bark of maples and birches. Fresh sap averaged 1.86 °B ( $\pm 0.75$ ,  $N=10$ ). Birds also licked evaporated sap from the bark surface below their open holes. The maximum concentration of this evaporated sap was 8.0°B, but averaged 4.62 °B ( $\pm 2.31$ ,  $N=5$ ). A typical feeding pattern for a bird was to arrive at a tree with open holes, start licking the trunk approximately 2 meters below the wound, work up the trunk to the open hole, and then spend 3-5 minutes lapping fresh sap before moving on to the next tree with an open hole.

In white birch, xylem-sap flow rate increased with ambient temperature (Spearman Rank Correlation,  $N=36$ ,  $Z=2.997$ ,  $P=0.003$ ; Fig. 1-1), but did not differ with the size of trees (Spearman Rank Correlation,  $N=36$ ,  $Z=-1.01$ ,  $P=0.31$ ). Average sap flow rate for birches was 2.89 ( $\pm 1.18$ ) ml/min from my 4.8 mm diameter drill holes. Sugar content of the sap

did not change with ambient temperature or tree size, but did vary between individual trees. When trees that were used by sapsuckers for xylem-sap extraction were compared to their nearest unused neighbors of the same species, I found that sapsuckers preferred trees with sap that had higher sucrose concentrations (Wilcoxon matched-pairs signed-ranks test,  $N=19$ ,  $P=0.04$ ; Fig. 1-2) but did not show a preference for higher sap flow rates (Wilcoxon matched-pairs signed-ranks test,  $N=16$ ,  $Z=-0.207$ ,  $P=0.84$ ). I was able to measure sap from only one maple tree that was used by sapsuckers for sap extraction. This tree yielded sap of a similar sugar concentration ( $2^{\circ}\text{B}$ ) but a much smaller rate of sap flow ( $0.15$  ml/min) than the birch trees that I measured.

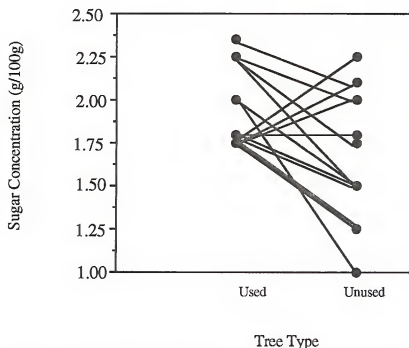


Figure 1-2. Concentrations of sucrose in xylem sap from artificial drill holes in two kinds of trees. 'Used' trees are ones in which sapsuckers made holes and fed from the exuding xylem sap. 'Unused' trees were neighboring trees of the same species and size as used trees but had not been attacked by sapsuckers.

I observed one bird feeding for two hours from four active holes in birch trees. One of these holes dripped sap at a rate of 1.29 ml/min. If all four holes yielded sap at a similar rate (and visual inspection suggested they did, although these holes were not accessible), then this feeding area could have provided 309.6 ml of dilute sap in the two hours that I observed this one bird. This male fed (dipped its beak into sap) 52 times/min in one 5 min interval of observation. During this same period of observation I saw this male make watery defecations at intervals that averaged 2.86 min ( $\pm 0.76$ , N=6). Although I was unable to collect and measure the sugar concentration of these defecations, I successfully measured defecations from other birds and found that the defecations were more dilute than the sap that they had been ingesting (Table 1-1).

Table 1-1. Sugar concentration of sap food and defecations of three individual yellow-bellied sapsuckers. The two adult males were feeding on xylem sap from birch trees. The captive juvenile was fed commercially prepared, diluted maple syrup.

INDIVIDUAL SAPSUCKER	SUCROSE CONCENTRATION OF SAP	DEFECATION INTERVAL	DEFECATION CONCENTRATION
Adult Male 1	3.25°B	2.31 $\pm$ 0.23 min (N=4)	0.25°B
Adult Male 2	2.27°B	2.86 $\pm$ 0.75 min (N=6)	--
Captive Juvenile	4.25°B	2.79 $\pm$ 1.05 min (N=6)	0.25°B

-- no data collected

### Discussion

The results suggest that sapsuckers exploit xylem sap as a source of food. Even when ingesting extremely dilute sap, they appeared to remove sugar from solution during digestion and made frequent defecations that were more dilute than the sap they were consuming. An alternative explanation for these watery defecations is that sapsuckers drink

copious amounts of water along with sap ingestion, thus diluting their resulting defecations. However, after hundreds of hours of observations, I never saw a sapsucker drink water, even though many of the territories under observation bordered a lake. In addition, a captive sapsucker never drank water when dilute solutions of sugar water were available at the same time. In short, sapsuckers most likely use xylem sap primarily as a source of food but may also gain water during the process. In further support of this hypothesis, sapsuckers preferred to attack trees with higher sugar concentrations in their xylem sap but had no preference for higher sap flow rates. If they were only using xylem sap for a source of water, this pattern of tree-use would not be expected. Yellow-bellied sapsuckers are in the same category as red squirrels and humans as seasonal harvesters of xylem sap. They too, take advantage of the early spring sap runs characterized by high sap pressure and relatively high concentrations of sucrose.

I found no correlations between sugar concentration of sap and tree size or ambient temperature, but I did find an increase in sap flow with temperature. Thus, I predict that sapsuckers should not show a pattern of harvesting xylem sap that is correlated with ambient temperature or tree size. I was unable to collect data on feeding patterns in relation to temperature or sizes of trees available and these questions remain to be explored.

Could sapsuckers rely on xylem sap as their only source of food during the early spring? No measurements of daily energy requirements of sapsuckers are available. However, an estimate of field metabolic rate for a similar-sized non-passerine bird can be made from an equation given by Nagy (1987). Sapsuckers, with an average mass of 47.6 g (pers obs. N=16), would require 85.2 KJ/d in food energy. Combining this energy requirement with the fact that carbohydrate food such as sap typically yields 17.15 KJ/g (Sturkie 1986), sapsuckers would need to consume 4.97 g/d of carbohydrates to meet their basic needs. The xylem sap from trees that the birds attacked averaged 1.9°B. If sapsuckers relied only on this sap as a source of food and can digest all but 0.25°B of the sugar in this sap, they would need to consume 299.4 ml/d of sap to survive. This suggests

that to eat only xylem sap, these birds would face enormous problems passing large volumes of sap through their systems and excreting excess water. Interestingly, I observed very high defecation rates. One female would have ejected 87.84 ml of watery defecation from her system in 6 h if she kept up the rates and amounts that I observed in one half-hour period. In addition to the problem of voiding water, enough xylem sap must be available in large quantities to support this kind of volume feeding. I observed very high flow rates from sapsucker holes. In one feeding area, I measured 77.5 ml/h from one sapsucker hole and this bird had at least four holes open at the same time. Assuming this sap has an average of 1.9°B sucrose, this adds up to 6.2 g of sugar available per hour in this one feeding area. Because this hourly rate value exceeds the daily requirements of a sapsucker, it may be possible for yellow-bellied sapsuckers to rely entirely on dilute xylem sap to fulfill their energy needs during this brief period in early spring.

Yellow-bellied sapsuckers probably have several ways to avoid the high costs of long periods of feeding and the need to void excess water necessary for exploiting xylem sap. First, like red squirrels, sapsuckers often took advantage of partially evaporated sap on the bark surface below their oozing sap holes. In many cases on warm dry days, I found that evaporation could concentrate the sugars two to six times the original levels of fresh sap. Second, some individuals were able to extract phloem sap from other tree species during this same time. Phloem sap is characterized by slower flow rates than xylem sap but has approximately ten times the sucrose concentration of xylem in early spring. Third, during the two-week period of xylem-sap feeding, sapsuckers may supplement their diet with insects. Although freezing nights were still common, a few insects were already active at this early time of year and I saw one male capture and eat a beetle. Defecations from most wild birds appeared clear and watery with no solid component. However, one female's fecal material contained insect parts, indicating she had supplemented her diet of xylem sap.

In conclusion, yellow-bellied sapsuckers feed on xylem sap for a brief period in early spring in Northern Michigan. While it appears they can maintain their energy reserves with

only this extremely dilute food source, these birds probably supplement their diet in ways that reduce the costs of rapid, constant feeding and elimination of excess water necessary for xylem-sap exploitation.

During the non-breeding season, sapsuckers feed on sap from a variety of trees throughout the central and southern U.S., Caribbean, and Central America. These trees are often attacked with horizontal lines of holes similar to those I observed for xylem feeding during the breeding season (McAttee 1911). Although this type of sap feeding has been studied very little, the pattern of holes left by these wintering and migrating sapsuckers suggest that they may be harvesting xylem sap.

This study is the first to my knowledge to report the heavy use of xylem sap by any bird, including sapsuckers. The rapid feeding and high defecation rates suggest a digestive system that may be specialized for harvesting solutes in plant sap. Future research on how these birds are able to select trees with higher sugar content, balance time budgets when long periods of feeding are necessary, and process large volumes of sap in their digestive systems (possibly ingesting more than twice their body weight each day) is needed to better understand the unusual adaptations of these woodpeckers.



## CHAPTER 2:

### A REVIEW OF ANIMALS THAT INCISE PHLOEM TISSUE AND EXTRACT PHLOEM SAP

#### Introduction

##### Overview

The fluid transported in phloem tissue, phloem sap, provides a relatively constant source of food for animals able to harvest it. Like nectar, phloem sap contains carbohydrates and some amino acids. However, unlike nectar, plants protect their phloem rather than offer it as a reward for pollination. In general, this protection comes in the form of physical barriers rather than chemical deterrents (Raven 1983). Only a few types of animals exploit phloem sap as food, even though phloem sap could potentially offer a more constant resource than the nectar of flowers. Perhaps relatively few animals eat phloem sap because plants protect their sap so well. Several recent reviews (Risebrow and Dixon 1986, Raven 1983) have shown that specialized adaptations are necessary for insects to harvest phloem sap. However, no comprehensive review has been completed for vertebrates that exploit phloem sap. In this chapter, I will first examine how vertebrates manage to tap directly into the stream of phloem sap and then explore the possible evolutionary pathways that may have led to exploitation of phloem sap by these vertebrates.

##### Phloem Sap and its Protection

Before examining the ways animals reach the sap stream, I need to review how phloem tissue functions and how it is protected. Phloem sap is an important transport fluid of plants that carries the products of photosynthesis from their source to a sink. Sinks can be parts of the plant that need nourishment for growth and reproduction or storage tissues. Thus, in the main trunk of a tree, phloem sap usually moves downward from the canopy to the roots. Phloem sap travels through chains of living sieve cells. Between each sieve cell

lies a sieve plate with small pores. Sap passes through the sieve pores when intact but upon injury sap flow is arrested as a result of several factors. 1) Sieve pores may partially collapse when the phloem tissue is cut. 2) Sieve pores clog with phloem proteins that move from the inside perimeter of the disrupted sieve cell to the sieve plate when a fast change in flow rate occurs with the disruption of cells by incision. 3) A carbohydrate called callose may form quickly in the sieve pores in response to injury (Salisbury and Ross 1992). When coupled with a thick layer of cuticle or bark, these self-sealing mechanisms of the sieve cells apparently protect phloem sap from most herbivores (Crafts and Crisp 1971). However, a few types of animals have managed to overcome these barriers and take advantage of phloem as a food resource.

Botanists have reported great difficulties in obtaining enough phloem sap for research from incisions into the phloem (Crafts and Crisp 1971). One solution to this problem is to take advantage of aphids and other homopterans which have stylets they can insert directly through protective tissue into a single phloem sieve cell. These stylets allow such insects to avoid the problems of clogged sieve pores when phloem pressure is disrupted (Risebrow and Dixon 1987). Botanists exploit this feeding mechanism by a technique to sever the aphid from its stylet and then use the exuding sap from the intact stylet for research (Kennedy and Mittler 1953).

But unlike homopterans, other animals can make incisions into the stream of phloem and obtain sap for food. I will call these animals "incision phloem-sap extractors" (IPSE). Clearly all IPSE must have the ability to cut through the barriers of thick bark and cuticle to reach the phloem. In addition, unlike homopterans, IPSE must also confront the problem of clogged phloem sieve pores. There are several alternative hypotheses for how IPSE might overcome this self-sealing mechanism of plants. First, botanists have noted that some species of plants have weaker self-sealing mechanisms than others (Martin and Sydnor 1987). Perhaps IPSE are able to select specific trees among the many available that have freely-flowing phloem sap and therefore avoid the need to overcome a self-sealing

mechanism. Second, IPSE may mechanically incise the phloem stream in a particular way, such as repeated fresh cuts into new, unclogged tissue, thus stimulating fresh sap flow. Fresh incisions into new phloem tissue would bypass any previously clogged cells and sap may then flow for a short time from new incisions before clogging. Third, IPSE may use saliva as an anticoagulant and reopen the clogged sieve pores by enzymatically clearing the protein and callose plugs. In the review below, I will discuss each of the IPSE individually, and explore the likely alternative adaptations they may have for this specialized feeding habit.

### Two Costs of Phloem Feeding

Although phloem sap contains some amino acids, it is often not enough to supply the needs of some herbivores (Raven 1983). Aphids and other homopterans solve the problem of getting a balanced diet by processing large quantities of phloem sap and excreting honeydew. Honeydew is mostly a solution of sugar and contains less protein than the original sap (Risebrow and Dixon 1987, Douglas 1993). Large nectar-feeding animals also face the same problem of amino acid limitation and must supplement their diet with insects or pollen (Baker and Baker 1983). Perhaps larger animals that exploit phloem must also have alternative food in their diet to provide a source of amino acids. In my review of phloem-feeding vertebrates I will examine the potential protein sources in the diets of these animals.

The main carbohydrate in phloem sap is sucrose (Zimmerman and Ziegler 1975). Some animals have limited abilities to digest sucrose in their diet (Martinez del Rio 1990). Flowers that contain sucrose-rich nectar are visited by different nectarivores than those that contain hexose-rich nectar (Baker and Baker 1983). Because phloem sap has sucrose, animals that specialize on phloem sap are expected to be able to digest sucrose efficiently. Thus, the evolution of phloem feeding may be more likely in animals that already have a digestive system that is adapted to a diet of sucrose. I will look for evidence of an ability to

exploit sucrose-rich foods in addition to the phloem sap in my review of phloem sap feeders.

### Incising Phloem-sap Extractors

1. Marsupial gliders. Yellow-bellied gliders (Petaurus australis) cut V-shaped grooves into boles of some eucalyptus species to extract sap. The lower edges of the grooves at the tip of the V are cut evenly and straight into the cambium layer. Sap collects at the base of the V where the gliders lick up the resulting pool of sap (Wakefield 1970, Henry and Craig 1984, Mackowski 1988). In many areas, gliders feed on sap throughout the year with peaks of feeding in certain months when other food types are less abundant (Smith and Russell 1982, Craig 1985, Kavanagh 1987). Although many species of Eucalyptus trees are often available to gliders, they use only one or a few species for sap extraction (Wakefield 1970, Smith and Russell 1982, Henry and Craig 1984, Craig 1985, Mackowski 1988, Goldingay 1991). Mackowski (1988) found that yellow-bellied gliders choose individual sap trees that have low cambial electrical resistance compared to other trees of the same species. This may indicate that particularly vigorous trees are used for sap exploitation because low cambial electrical resistance is associated with both higher levels of solutes or larger quantities of sap. Gliders did not prefer trees with more sucrose in their sap in one study (Henry and Craig 1984), but in another they preferred trees with a higher percentages of sucrose (Goldingay 1987). These animals also exploited trees at times when the trees had higher sap flow rates (Goldingay 1987, 1991). Mackowski (1988) speculated that yellow-bellied gliders may use saliva to stimulate sap flow because incisions with a razor blade failed to yield sap in the same sap trees, although no definitive tests were made. In support of this conjecture, several authors have described the way gliders repeatedly lick sap incisions during feeding bouts, possibly adding saliva to the wounds (Goldingay 1987, Kavanagh 1987, Mackowski 1988). Yellow-bellied gliders continue to feed on sap from the same trees for extended periods of time by the repeated gouging of the bark to enlarge current incisions or make new ones (Goldingay 1987).

Less is known about the sugar glider (P. breviceps) than the yellow-bellied glider but it is clear that sugar gliders also incise the bark of eucalyptus trees and extract sap. Smith (1982) found that sugar gliders made new wounds frequently in sap trees during active feeding times and used individual trees for long periods of time. When feeding, sugar gliders chewed the sides of the wounds but it is not clear whether this behavior saliva stimulated sap-flow (Smith 1982). Although some questions remain unanswered, more is known about the sap-extracting behavior of gliders than any of the other IPSE in this review. It appears that they may use all three of the hypothesized methods for sap extraction including choice of specific trees, repeated incisions, and use of saliva.

2. Squirrels. Gray squirrels (Sciurus vulgaris) in Europe strip bark from maples (Acer spp.) and pines (Pinus spp.) and then eat the exposed phloem tissue and drink sap from these wounds (Pulliainen and Salonen 1963, Kenward 1982). Kenward (1982) found that squirrels preferred trees with more sap but not with sweeter sap. Pulliainen and Salonen (1963) noted that not all individuals in a population foraged in this way, but those that did pulled off strips from successively higher positions on the main bole of the tree. Little else is known about this sap-eating habit. It is not known whether the squirrels are simply taking advantage of particularly saturated phloem tissue or if they actually stimulate the flow of sap in some way. Thus, gray squirrels may be able to extract sap by selecting specific trees and repeatedly making fresh tears into phloem tissue. However, stripping bark may not have the same effect of bypassing clogged tissue as does cutting through the bark.

3. Marmosets. Although no one has determined the ratio of gum to sap in their diet, Ramirez et al. (1978) concluded that pygmy marmosets, Cebuella pygmaea, probably take both gums and phloem sap when they dig holes in the bark of trees with their specialized teeth. C. pygmaea restrict much of their exudate-feeding activity to one or a few trees within a territory (Soini 1988, Soini 1993), indicating that certain individual trees may be more conducive to sap extraction than others. Coimbra-Filho and Mittermeier (1975) suggest that C. pygmaea have specialized teeth as an adaptation for exudate feeding but no other

information is available on unique adaptations C. pygmaea may have for phloem sap extraction.

Members of the genus Callithrix also probably take some phloem sap along with gum when incising the boles of trees for food (Lacher et al. 1984, Stevenson and Rylands 1988). Again, much remains unknown about phloem sap extraction in this genus and many authors do not make the distinction between gum and sap as food (Coimbra-Filho and Mittermeier 1975, Rylands 1985, Rylands and de Faria 1993). Callithrix jacchus penicillata prefers specific species of trees for exudate extraction and attacks each species in a different manner (Lacher et al. 1984). This pattern indicates specialized behavioral adaptations for exudate feeding in this species. However, until it is determined whether these animals obtain gum or phloem sap from their trees, any specific adaptations for extracting phloem through incision into the stream of sap cannot be determined.

**4. Lemurs.** At least one species of lemur, Phaner furcifer, specializes on plant gum and appears to extract phloem sap occasionally (Charles-Dominique 1977). Although no information is available about exactly how P. furcifer extracts sap, observations have been made of this animal getting a thin sap-like substance from reniala trees (Adansonia spp., Bombacaceae) (Charles-Dominique and Petter 1980). Many other species of trees yield gum when wounded by P. furcifer, but only Adansonia yields sap. This suggests that the only way this animal can extract sap is by exploiting this particular species, which might have weak phloem-sealing properties. Thus, while P. furcifer clearly has specialized dentition for exploiting gums (Petter et al. 1971), it may have no unique phloem-extracting adaptations beyond the ability to select specific trees.

**5. Humans.** The human agricultural industries of palm sugar, fermented toddy, and tequila production all involve the extraction of phloem sap from monocotyledonous plants (see Van Die and Tammes 1975 for a review). In these cases, people extract phloem sap by taking advantage of the unique properties of some monocot stems, especially inflorescence stalks, that allow sap to exude copiously from cut stems. The specific technique involves

renewing the exuding wound at least once a day by making fresh cuts into the phloem tissue in the direction of the phloem source. No additional chelating agent or other substance is used to enhance sap flow. The tapping period lasts for several months in many cases. In addition to these monocotyledonous sources of sap, ash trees (*Fraxinus* spp., Olivaceae) in Southern Europe are tapped during the hot season for their sap. The exuded sap is left to dry on the tree and when harvested is called manna. As in palms, new incisions are made each day above the previous incisions in the boles of the tapped trees (Huber 1953, Van Die and Tammes 1975, Donkin 1980). As noted above, botanists have reported problems obtaining phloem sap from incisions into most trees and often employ the stylets of aphids for sap collection (Salisbury and Ross 1992). Thus, it appears that special techniques or adaptations would be necessary for harvesting phloem from most trees and people are only able to obtain large quantities of sap from specific species of trees.

**6. Woodpeckers.** Sapsuckers (*Sphyrapicus* spp.) specialize on sap feeding during both the breeding and non breeding seasons. They attack over 200 species of trees throughout North America (McAtee 1911, Rushmore 1969), but focus on only a few individuals of a few species for sap collection at any one time (Foster and Tate 1966, Tate 1973). Within one season, new sap incisions are made above old ones in the bole of exploited trees (McAtee 1911). Yellow-bellied sapsucker holes often ooze copious amounts of sap that many other organisms exploit for food (Foster and Tate 1966, Daily et al. 1993) and it appears that they select specific trees and make fresh incisions into phloem tissue to help extract the phloem sap from trees. In addition, members of the Picidae have modified salivary glands that produce sticky saliva to assist in insect extraction (McLelland 1979). Sapsuckers may have the ability to use their saliva for stimulating sap flow. To date, no published reports have addressed sapsuckers' use of saliva.

Although their holes were once attributed to sapsuckers, research has shown that acorn woodpeckers (*Melanerpes formicivorus*) attack several species of oak trees for their sap (MacRoberts 1970, MacRoberts and MacRoberts 1976, Kattan 1988). Kattan (1988)

found that acorn woodpecker groups selected one or two individual trees from many on their territory to use as sap sources. New sap holes are usually made on boles of previously used trees. Acorn woodpeckers begin new holes about one month before they start to eat sap from these holes (MacRoberts and MacRoberts 1976). Holes are spread in a characteristically even pattern over a large part of a tree trunk (MacRoberts and MacRoberts 1976, Kattan 1987). Little is known about how acorn woodpeckers actually stimulate sap to flow from their sap trees (W. Koenig, pers. com.), but saliva is again a possibility. A few other species of woodpeckers have been reported to make and/or feed from sap holes (White 1873, Witherby et al. 1948, Gibbs 1983, Ripley 1989) in trees, but these reports are brief observations at best and little is known of the pattern or methods of wounding by these other species.

### Discussion

It is clear that few animals have been observed to extract phloem sap by incisions into the vascular stream of a tree. Perhaps several adaptations are necessary to overcome a plant's protection of its phloem sap before phloem sap can be harvested. All of the animals in this review have the ability to chew or puncture the thick outer layer of bark that protects phloem tissue. In addition, most have the behavioral adaptations to continue enlarging sap incisions or to make new sap incisions above old ones, thereby incising fresh, undisturbed phloem cells and bypassing any clogged sieve pores in old incisions. In all species that have been observed in detail, it appears that the selection of individual trees may be an important behavioral adaptation for successful sap extraction. Finally, sugar gliders, and possibly other sap eaters, may use their saliva as an anti-clogging agent to clear blockages of p-protein and/or callose and thus use a biochemical adaptation for exploiting sap.

Information on IPSE is sparse. Perhaps because such specializations are necessary for phloem extraction, only the animals described in this review may be able to take direct advantage of this food resource. Animals without the ability to stimulate sap flow can steal



it from extractors or ingest it by eating the tissue that contains it. Both of these strategies are common. Numerous animals are associated with the sap incisions of the extractors in this review, including sugar gliders (Smith 1982), sapsuckers (Foster and Tate 1966, Kattan and Murcia 1985, Williams 1990, Daily et. al. 1993), and marmosets (Soini 1988), and often steal sap from them. In addition, many animals such as rodents, rabbits, bears, and birds other than sapsuckers gnaw or cut through bark and eat the phloem and cambium tissues, but do not stimulate sap flow (Kilham 1959, Pulliainen and Salonen 1963, Suzuki 1965, Radwan 1969, Farentinos et al. 1981, Sullivan et al. 1986, Snyder 1992). Although these bark-eaters could be gaining nutrition from the tissues themselves (Haack and Slansky 1986, Risebrow and Dixon 1986), an alternative explanation is that they are harvesting as much phloem sap as possible given that they possess no specialized adaptations for extracting the sap. Thus, the existence of many sap stealers and bark eaters suggests that the extraction of phloem sap from trees by incising the sap stream may require specializations that most animals do not possess.

In addition to the problems of extracting phloem sap by incision into phloem tissue, the need for alternative protein sources and ability to digest sucrose efficiently may be costs of exploiting this type of food. Each of the six groups or species of IBSE discussed above has a source of protein in its diet in addition to phloem sap (Table 2-1). I also found that all of these IBSE ate other food types that contained sucrose, including the honeydew excretions of Homoptera and nectar. It would be interesting to test how well these IBSE digest sucrose. I predict that all will be efficient handlers of this disaccharide.

Perhaps a suite of evolutionary precursors is necessary before phloem extraction can evolve. Other taxa that have the strength and appropriate morphology to incise bark and expose phloem tissue, but have not been observed extracting sap include rodents (with the possible exception of a squirrel, see above), lagomorphs, and ungulates. Perhaps they are not able to exploit phloem sap because their diets are not high enough in protein to make sap feeding beneficial. These animals may also be less efficient at digesting the sucrose in

phloem sap if they have no other dietary experience with sucrose-containing food. If additional research reveals other phloem feeders, I would expect them to come from groups with high levels of protein and sucrose in their diet.

Table 2-1. Vertebrates that extract sap by incising phloem tissue of trees, other dietary items, and their known methods of sap extraction.

SPECIES	SOURCE OF PROTEIN	OTHER DIETARY SUCROSE	REFERENCES
Yellow-bellied glider <u>Petaurus australis</u>	beetle larvae, other arthropods, pollen	honeydew, nectar	Kavanagh 1987 Henry and Craig 1984
Sugar glider <u>Petaurus breviceps</u>	arthropods, pollen	honeydew, nectar	Smith 1982
Gray squirrels <u>Sciurus vulgaris</u>	insects	buds and flowers	Pulliainen and Saolnen 1963
Pygmy marmoset <u>Cebuella pygmaea</u>	small arthropods	nectar, flowers	Ramirez et al. 1978 Soini 1988
Common marmoset <u>Callithrix jacchus</u>	arthropods, snails, small vertebrates	flowers	Stevenson and Rylands 1988
Forked-tailed lemur <u>Phaner furcifer</u>	nocturnal insects	'licks' flowers, honeydew	Charles-Dominique and Petter 1980
Humans <u>Homo sapiens</u>	many sources	perhaps first exploited sap processed by homopterans	Donkin 1980
Acorn woodpecker <u>Melanerpes formicivorus</u>	small arthropods	flowers	MacRoberts and MacRoberts 1976
Yellow-bellied sapsuckers <u>Sphyrapicus varius</u>	small arthropods	honeydew	Greenberg et al. 1993 Tate 1973

However, the preadaptations of the presence of dietary protein, ability to digest sap and ability to make incisions into bark cannot explain entirely the evolution of IBSE. Within the Picidae species appear to have these preadaptations but do not extract sap. All woodpeckers eat insects and can cut through bark (Short 1982). Although no woodpeckers other than sapsuckers have been observed feeding from honeydew secretions, analysis of the stomach contents of several other woodpecker species reveals homopteran insects in their diet (Beal 1911). Further, five species of woodpeckers other than sapsuckers have

been observed feeding on sap from sapsucker sap incisions (Foster and Tate 1966), indicating that they have no problem digesting sucrose. Perhaps the evolution of the specialized sap-extraction adaptations was driven by the need for supplementary food in times of low food availability. Acorn woodpeckers and yellow-bellied gliders both live in very seasonal habitats and exploit sap when the availability of other foods is low (McRoberts and McRoberts 1976, Kavanagh 1987). Although sapsuckers do not appear to experience periods of low food availability during the year, they may have been able to avoid competition with other woodpeckers in their range by exploiting phloem sap as a novel food resource.

Given that phloem sap can provide a source of food, but requires specialized adaptations to obtain, the animals able to extract sap may serve as keystone species within their communities, providing many other animals with a good food resource. Insect phloem feeders with their exuded honeydew often are involved in complex interactions with other animals that exploit their sap-extracting abilities (Greenberg et al. 1993, Way 1963). Daily et al. (1993) suggested that sapsuckers serve as important keystone species in their community and several have suggested that hummingbirds actually increase their breeding range as a result of their exploitation of sapsucker sap (Miller and Nero 1983, Sutherland et al. 1982, Southwick and Southwick 1980). Little is known of the communities surrounding the sap holes of sap-extracting mammals such as sugar gliders, marmosets, and humans, but I would expect some interesting and complex interactions.

Many questions about exact mechanisms remain unaddressed. These include the use of saliva as an anti-clogging substance in sap holes, specialized adaptations for the digestion and processing of sap, implications for territoriality and other social consequences of using single food trees over long periods of time, and coevolution between trees and extracters. I will explore some of these questions with yellow-bellied sapsuckers in upcoming chapters but more research is needed on the feeding habits of the wide variety of sap-extracting vertebrates.

## CHAPTER 3: SAP-TREE SELECTION BY YELLOW-BELLIED SAPSUCKERS

### Introduction

#### Overview

Patterns in host-plant selection by herbivores can be affected by genetic variation and environmental conditions of the host (Denno and McClure 1983, Fritz 1990, Fritz and Simms 1992). Although much research has focused on the underlying factors influencing disease resistance in plants, especially in agricultural systems (see Pilson 1992 for review), very few studies have attempted to separate the genetic and environmental components of herbivore preference in nature (Kennedy and Barbour 1992). Herbivores that eat sap may be very selective in their choice of host plants because nutrient levels and plant secondary compounds can have large effects on the quality of their diet (Whitham 1983).

Yellow-bellied sapsuckers harvest phloem sap throughout the year (Beal 1911). They select individual trees within each of several preferred species for the extraction of phloem sap during the breeding season (Kilham 1964; Lawrence 1967; Rushmore 1969, Tate 1973). Observations of other sap-eating vertebrates have shown that these animals also favor particular trees for sap extraction (see Chapter 2). What qualities yellow-bellied sapsuckers find desirable in the individual trees that they attack and how they obtain sap remain unknown. I will explore four hypotheses about tree selection and test whether selection of specific trees could help to explain how sapsuckers get sap to flow from their incisions.

#### Travel Distance

Yellow-bellied sapsuckers feed their nestlings a mixture of insects and sap (Foster and Tate 1966, Lawrence 1967). The unusually long nesting period of 29 d coupled with the need for sap add up to a large number of trips between sap trees and the nest cavity over the course of the breeding season. Optimal foraging theory suggests that animals should minimize traveling distance to conserve energy (Stephens and Krebs 1986). Thus, the travel-distance hypothesis predicts that sapsuckers will choose trees for sap extraction that are as close to the nest as possible to minimize the energy needed to carry food to nestlings. Because cavities can be constructed in only a few trees (see introduction) and availability of nest sites is often limited for woodpeckers (Welsh and Capen 1992), the distance between the nest and sap trees is most likely to be influenced by the choice of sap trees and not the choice of nest trees.

#### Microsite

In addition to the importance of location for considerations of traveling distance, a tree's microsite can influence its quantity and quality of phloem sap. Microhabitat factors such as water and light availability have an effect on plant sap (Nichols-Orians 1991) and influence both how much water is available for sap transport (Hall and Milburn 1973) and how much photosynthate can be sent down a tree's trunk for storage in the root system (Dale and Sutcliffe 1986). The microsite hypothesis for tree selection predicts that the trees that sapsuckers select for sap extraction will grow in similar microsites with common properties, such as moist soils, high light intensity, and low tree density.

#### Individual Differences Between Trees

Variation among individual trees, in addition to microsite, can lead to differences in sap quantity, quality, or in how easily sap can be extracted (Gabriel 1982). Sapsuckers may prefer specific individual trees not necessarily because of their location but because of individual variation in sap quality. Such a pattern in tree preference could result from selection for higher quality sap, such as high amino acid or sugar content (White 1984, Chapter 1), or an avoidance of sap that may be protected by secondary chemicals in certain

individual trees (Snyder 1992). The individual-variation hypothesis suggests that sapsuckers should choose tree trunks that are members of the same clone or individual stems of the same clump, but not several independent individuals growing in a particular location. Several other herbivores have this type of preference for specific genotypes in their host plant (see Linhart 1989 for a review).

#### Wounded Trees and Historic Use

Kilham (1964) suggested that yellow-bellied sapsuckers may concentrate their sap-extraction activities on only a few trees to enhance the sap flow through the effect of girdling. He postulated that phloem sap would accumulate above an old wound and increase sap availability. The wounded-tree hypothesis predicts that sapsuckers should prefer trees with old wounds and may intentionally wound trees during the current breeding attempt in preparation for the next breeding season if they reoccupy the same territory. New wounding would occur in current areas of activity thus creating a clumped pattern of tree use after several years of continuous occupation of an area. This hypothesis works only if birds or their offspring show site fidelity from year to year and, indeed, Lawrence (1967) found that in a color-marked population some birds returned to breed in the same territory in successive years.

#### Methods

This study was conducted on the University of Michigan Biological Station property (see chapter 1 for description). Yellow-bellied sapsucker activity was patchily distributed and concentrated in areas with rich deciduous forest (Foster and Tate 1966). I identified all major sap wells used for sap extraction in four main areas of activity during both the 1992 and 1993 breeding seasons. Sap wells were defined as clusters of 100 or more holes on the boles or large branches of living trees and were located by visual survey of the forest and by observing the activity of foraging sapsuckers. For each sap well I noted its location on the tree (whether on main bole or major branch), distance to the nearest node of a live branch, presence of old wounds below the holes made in the current year, and height above ground.

For some sap wells, I measured the tree's circumference at the well, but for other sap trees I was only able to measure the circumference at breast height. In addition, I noted whether the tree was growing in a clump or as a single tree. A clump was defined as having two or more boles at breast height that originate from the same root stock. Active nest cavities were located on the territories in the study areas by listening for sounds of cavity excavation in April and May of both years, or by observing the behavior of birds on their territories.

I compared the properties of trees used for sap extraction with those that remained unused. I defined 'used trees' as those with at least one active sap well. Occasionally more than one sap well was active in a tree at the same time. If several stems in one clump had sap wells, I collected one data point only from the clump, assuring that each data point came from an independent plant. Likewise, 'unused trees' were defined as those without major sap wells that were unconnected to any trees with sap wells.

To test the hypothesis that birds used particular trees because they were close to the nest cavity, I observed whether the trees used for sap extraction were as close as possible to the nest tree. I located trees with active sap wells and compared their distances to the nest with distances to the nest of unused, potential sap well trees. I first measured distances between active sap wells and the nesting cavity on each territory by pacing and converting paces to distance in meters. Next I located the closest unused tree to the nest cavity that was of the same species and of equal or greater CBH as each sap-well tree. Distances between the unused trees and cavities were compared to the distances between the used trees and cavities with a paired Wilcoxon matched-pairs signed-ranks test.

In 1993 I tested the hypothesis that used trees were chosen for their particular microhabitat location. I paired used trees with their closest unused neighbor of the same species of equal or greater DBH located in the direction of the nest cavity. I compared the microhabitat of these pairs by measuring soil moisture and tree density. The soil moisture data were collected by taking a sample of approximately 50 g of surface soil, under the leaf litter but not more than 5 cm deep, and 1 m from each tree. Wet weights were compared to

dry weights to calculate percent moisture of each sample. Tree density was calculated by counting all live tree trunks  $\geq 5$  cm DBH within a 5 m radius of the focal tree.

I used the same pairs of used and unused trees as above to compare properties of individual trees used for sap extraction. I characterized individual trees by five additional variables: health, canopy size, cambial electrical resistance, bark moisture, and bark thickness. Tree health was estimated with an index health score: 1=most branches dead and only a few living leaves, 2=more than half the branches dead and all leaves reduced in size or yellowish, 3=up to half the branches dead and at least some full-sized leaves on tree, 4=less than one quarter of the branches dead and some leaves reduced, 5=completely healthy with no dead branches and all full-sized leaves. Canopy size was estimated with a concave spherical canopy densiometer. Two estimates were taken on opposite sides of the focal tree's base and then averaged. The densiometer was held against and perpendicular to the bole of the tree at breast height in such a way that exactly one half of the concave mirror was filled with the reflection of the tree's bole. The densiometer's mirror was marked with 24 square quadrats. The canopy size was then estimated as the number of empty quarter quadrats on the remaining half of the densiometer's mirror that reflected the crown of the tree. Values could range from a minimum of zero (completely full canopy) to 48 (no branches or leaves on that side of the tree). Cambial electrical resistance was determined in a manner similar to that used by Shigo and Shigo (1974) using a Micronta digital multimeter, model 22-171A. Stainless steel electrodes fixed in position 2 mm apart were inserted into the bark and the minimum electrical resistance (ER) of a pulsed electrical current was recorded for three locations at breast height on the trunk of each focal tree. Cambial ER was used by Mackowski (1988) as a measure of tree vigor in his study of tree selection by yellow-bellied gliders. Lower values of ER would be expected in trees with either more phloem sap or sap with a higher solute content. Two plugs of bark which included all tissue between the outer surface and the sapwood were collected with a grommet punch at breast height (see chapter 4) from each focal tree. Plugs of bark were



weighed, dried, and weighed again for a measure of bark moisture content. Bark thickness was measured as the distance in mm between the outer surface of the bark plugs and the sapwood.

To test the question of whether the use of specific trees could help to explain how sapsuckers are able to obtain free-flowing sap from their incisions, I attempted to extract sap from both used and unused trees. A variety of incisions were made, including cutting through the bark to the sapwood with a steel knife blade, drilling 5, 6, and 9 mm holes through the bark with sharp steel wood bits, chiseling square holes with 6 and 13 mm steel straight-edged chisels, and punching holes through the bark with a grommet punch (as described above). Incisions were made in a variety of locations on experimental trees, including breast height, the center of sap wells, 1-2 mm above active sap holes, and approximately 10 cm above sap wells.

### Results

Of 36 active sap-well trees that I observed in 1992 and 1993, 17 were in birch, 8 in red maple, 6 in juneberry, and 5 in big-tooth aspen. Two of the sap wells were constructed on large branches and the rest were located on the main bole of the tree. Sapsuckers extracted sap from trees that were located in clumps that included other used trees more often than they attacked single trees or trees located in otherwise unused clumps. Of 19 independent woody stems originating from different root stock and containing sap wells, 13 were in clumps with other used trees. Sap wells were located at an average height of 7.13 m ( $\pm 3.47$ ,  $N=19$ ) on trees and 18 out of 19 were within 1 m of the node of a live branch. Sap-well trees observed in 1992 had an average circumference at the sap well of 50.7 cm ( $\pm 15.5$ ,  $N=17$ ). Trees that had active sap wells in 1993 had an average circumference at breast height of 64.2 cm ( $\pm 22.5$ ,  $N=18$ ).

Yellow-bellied sapsuckers chose trees for sap extraction that were farther from their nest than unused trees of the same species and size (Wilcoxon matched-pairs signed-ranks test,

$n=24$ ,  $p=0.0001$ ). Trees used for sap collection were located an average of 64.9 m farther from nests than unused trees of the appropriate size and species (Fig. 3-1).

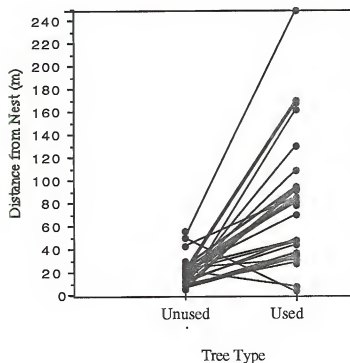


Figure 3-1. Paired comparisons between the distance of nest trees to trees used for sap extraction and the distance of nest trees to the closest unused trees of the same size and species as the tree used for sap extraction.

Measurements of microhabitat, including soil moisture and tree density, did not differ between trees used for sap extraction and their nearest unused neighbor of the same species and equal or greater DBH (Table 3-1). In addition, measurements of individual variation such as crown size, bark thickness and bark moisture also did not differ between used and unused trees. However sap trees were less healthy (Wilcoxon matched-pairs signed-ranks test,  $n=14$ ,  $p=0.003$ , Fig 3-2) and tended toward a lower ER (Wilcoxon matched-pairs signed-ranks test,  $n=18$ ,  $p=0.0854$ ) than unused trees.

Table 3-1. Comparisons between trees used for sap extraction and neighboring unused trees. All p-values are from Wilcoxon matched-pairs signed-ranks tests. Values for sap and non-sap trees are shown as means with standard deviations.

VARIABLE	SAMPLE SIZE	MEANS FOR USED TREE	MEANS FOR UNUSED TREE	P-VALUE
<b>Microhabitat</b>				
soil moisture (%)	17	12.63 $\pm$ 5.25	14.73 $\pm$ 6.29	0.4631
tree density (number per 20m <sup>2</sup> )	16	7.8 $\pm$ 3.2	7.0 $\pm$ 3.8	0.4777
<b>Individual differences</b>				
crown size (no. open quarters)	16	4.2 $\pm$ 3.2	5.4 $\pm$ 4.1	0.3133
bark thickness (mm)	18	6.5 $\pm$ 2.5	6.5 $\pm$ 4.1	0.7628
bark moisture (%)	19	37.10 $\pm$ 6.42	36.64 $\pm$ 4.73	0.6008
health (index value)	19	3.2 $\pm$ 1.1	4.5 $\pm$ 0.9	0.0030
cambial ER (k-ohms)	18	46.7 $\pm$ 27.5	92.2 $\pm$ 181.8	0.0854

Old scars left by wounds from previous years were sometimes difficult to see, especially in used trees that could not be climbed, forcing observation from the ground. Of 20 individual sap wells I observed in 1993, at least 17 were constructed immediately above scars left by sapsucker holes from previous years. Only one of the remaining three sap

wells was unmistakably in a fresh, unscarred tree; the other two were too high to determine the presence of scars left by old wounds.

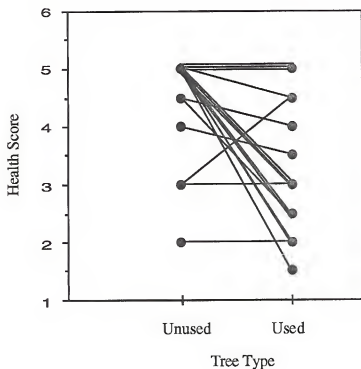


Figure 3-2. Paired comparisons between the health scores (as defined in text) of trees used for sap extraction and those of unused trees.

I obtained sap only when my incisions were made 1-2 mm above active sapsucker holes. Incisions made 10 cm or more above sap wells of these same trees did not yield sap. In no other situation did sustained sap flow occur from my incisions in either used or unused trees.

### Discussion

Yellow-bellied sapsuckers did not prefer to extract sap from trees close to their nest trees even though trees of the appropriate species and size were often available near the cavity sites. Thus, I can reject the hypothesis that sap trees were selected on the basis of

minimizing travel distance during the breeding season. Sapsuckers traveled great distances to reach them.

One factor that influences phloem sap is the microhabitat of the sap tree (Dale and Sutcliffe 1986). However, I found no indication that sapsuckers preferred trees in wetter sites or trees growing under less dense conditions which might indicate that they received more light or experienced less competition. Therefore, I suggest that sapsuckers may prefer trees for their individual qualities and not for their microhabitat or location in relation to the nest cavity.

I found a striking difference between the health of trees that sapsuckers used for sap extraction and neighboring unused trees. Trees in poor health could be either a cause of sapsucker preference or an effect of their attack. Trees that are in poor health or beginning to senesce are likely to have higher levels of amino acids in their phloem sap (see White 1984 for review). Because nitrogen is often a limiting nutrient for phloem-feeding animals (Fitter and Hay 1987), sapsuckers may prefer to eat sap from dying trees because this sap offers a more balanced nutrition than sap from healthy trees. On the other hand, the difference in tree health that I detected may have resulted from the sapsuckers' wounding efforts and not from tree preference. Sapsuckers may choose healthy trees for attack but as they slowly girdle the tree with their wounds, the tree dies. Such a scenario was suggested by Tate (1973) when he found that an average of 3.75 sap trees died per year on one territory he followed for 4 yr. However, while it is clear that the trees that sapsuckers attack are less healthy than surrounding trees, without more information, conclusions cannot be drawn about whether sapsucker use is a cause or effect of this phenomenon.

The fact that sapsuckers preferentially attacked multiple stems in clumps of trees that were members of the same clone suggests either that genetic differences between clones underlie tree preference or that the available trees of the correct species are a limited resource and are located in clumps. Some results collected in a student project at the biological station suggest that the former is more likely. M. Okonieski (pers. com.) found

that only 42 % of the trees of the appropriate species that were available on three sapsucker territories were used for sap extraction. Her result, coupled with my finding that sapsuckers favor specific clones or clumps of trees for attack, suggests that genetic differences between trees could explain tree preference in these birds. However, given my results of a preference for unhealthy trees, the same pattern of use could occur if diseases or senescence affected whole clones at the same time and not single stems. Thus, I cannot clearly separate the effects of genetic differences and variation in pathogen attack on tree selection by sapsuckers.

I found no significant differences between used and unused trees in cambial electrical resistance, bark moisture, crown size, or bark thickness. Thus sap quality may be influenced by the underlying genetics or disease state of the trees, but without more information I cannot determine what exactly the birds preferred in the trees that they used for sap extraction. My failure to induce sap flow from incisions in both used and unused trees indicates that sapsuckers do not prefer specific trees for their poor phloem-sealing properties. Other possible differences between used and unused trees that remain to be explored are content of plant secondary compounds, solute content of the sap, production of exudates to seal wounds, and the overall vigor of a clone.

At least 85 % of all major sap wells observed during this study were constructed above scars left in the phloem as a result of old wounds. As predicted by the wounded-tree hypothesis, sapsucker preference for individual trees may be a result of historic use of particular trees in the area. If, during the breeding season, a few holes are made to wound the unused trees surrounding the current active sap well, then in the following year major sap wells could be constructed above these wounds. Such a scenario could explain why sap wells tend to be located in clumps of trees, because after a few years of such girdling, old and new used trees would be centered around areas of high activity. In the next chapter, I will explore the value of having previously wounded trees on a territory.

By testing four alternative hypotheses for sap tree preference in yellow-bellied sapsuckers, I found evidence that sapsuckers choose trees because of their individual properties, rather than their location. A strong preference for specific senescent or diseased individuals of certain species would have long-term implications for the population biology of yellow-bellied sapsuckers. The trees that sapsuckers prefer are early-successional species which can not germinate under shady forest conditions (Elias 1980). Thus, for new trees to become available as current sap-well trees die each year, sapsuckers must have access to former gaps or forest edges to find the trees they need. The current forest over much of North Eastern North America is a second growth forest with many old senescent edge and gap species. Thus, sapsucker populations may be higher now than in pre-settlement times when large tracts of old-growth forest dominated the area. More trees appropriate for sap extraction are likely to be available now than in the pre-settlement forest.

## CHAPTER 4:

### REPEATED WOUNDING AS A POSSIBLE BEHAVIORAL ADAPTATION FOR STIMULATING PHLOEM SAP FLOW

#### Introduction

Phloem sap provide a relatively constant source of carbohydrates for animals able to harvest it. However, plants protect phloem sap with self-sealing properties that prevent it from flowing freely from an incision (Kallarackal and Milburn 1983). Many insects have adaptations to pierce phloem tissue and extract sap without disrupting phloem sieve cells (Raven 1983), thus avoiding the problem of blockages to sap flow caused by the rush of cellular contents such as phloem protein and callose out of the cells or the cooapse of seive pores upon injury. The few species that exploit phloem sap by making incisions into phloem tissue appear to have some specializations for harvesting sap (see Chapter 2).

Botanists have noted the phenomenon of sap accumulation in tissue above a girdle or major wound in the woody stems of plants (Salisbury and Ross 1992). In this chapter I will address the hypothesis that sapsuckers can cultivate their sap resource by repeatedly wounding the main bole of a tree in a pattern that blocks the phloem stream and forces the accumulation of phloem sap above these wounds. Thus, as they make new sap incisions above old ones, sapsuckers tap into fresh tissue that has more sap than is contained in tissue from undisturbed boles. Kilham (1964) noted that sapsuckers often attack the boles of trees above old wounds, but no research has tested whether sapsuckers can wound trees in a way that will promote the availability of their food resource.

Sapsucker sap holes can produce copious amounts of sap. Trees with several active holes often have wet trunks for many days or weeks because sap overflows the holes and drips down the tree (Foster and Tate 1966). In the previous chapter, I found that sapsuckers



clearly chose individual trees for sap extraction. However, most of my attempts at obtaining sap by incision into those trees were futile, suggesting that there is more to extracting sap successfully than simply choosing the 'right' tree. The few trials where sap flowed from my holes occurred when I made incisions just above a sapsucker's hole that flowed with sap in a major sap well. This suggests that through their wounding techniques, sapsuckers can increase the probability that sap will flow from tissue above their wounds. In this chapter I will focus on wounding method as a possible behavioral adaptation of yellow-bellied sapsuckers that allows them to obtain phloem sap more easily.

### Methods

All observations and experiments were conducted on the property of the University of Michigan's Biological Station in Cheboygan county during April through July of 1992 and 1993. In this area sapsuckers harvest sap from a series of tree species as the season progresses, but during the period of heaviest sap exploitation they concentrate on four species; white birch (Betula papyrifera), red maple (Acer rubrum), juneberry (Amelanchier spp.) and big-tooth aspen (Populus grandidentata) (Tate 1973).

In the following descriptions, I refer to a cluster of at least 50 wet or dry holes in the bole or large branch of a tree as a sap well. A wet hole has sap flowing from it. Dry holes may have had flowing sap at some time. In four major sap wells (one Amelanchier, two Populus, and one Betula), I followed the accumulation of new holes made by sapsuckers through time and periodically measured sap flow rates and sugar content of the sap. Sap flow rates were measured using a 1 ml tuberculin syringe. Each hole was completely evacuated and then after a timed interval, all the new sap that had collected in the hole was measured. The major solute in the sap was assumed to be sucrose (Salisbury and Ross 1992), and its concentration was measured with an American Optical 10431 T/C Hand Refractometer with a range of 0-55°B sucrose per 100 g water. I converted g/100 g to g/100 ml using the values suggested by Bolten et al. (1979).

### Experiment with Natural Sap Wells

To test the hypothesis that sapsuckers increase the potential to harvest sap from a tree repeated wounding, I set up an experiment to exclude the birds from some of their sap wells. At the beginning of the breeding season, I identified 17 pairs of sap wells that had the potential to be used for sap extraction in the current breeding attempt, but were not yet a focus of sap harvest. In another part of my study, I found that at the beginning of the breeding season, each territory can have 7 to 21 old sap wells in living trees and that the birds preferentially attacked these as their main sap wells for the season (see Chapter 6). I matched the pairs of old sap wells by size, tree species, territory, and microsite. I then covered the entire cluster of holes on one member of each pair with tar paper and duct tape. This prevented the birds from making new holes in or above the covered wells.

Covers were left in place during the most active part of the breeding season and removed after 43-58 d. At this time, all old and new holes were counted in each well. Because of the self-sealing properties of trees, I was unable to collect phloem sap from trees by incisions into the phloem stream (see chapter 3); therefore, I could not compare sap flow rates and sugar content between treatments. As a solution to this problem, I measured the percent moisture in plugs of bark and phloem tissue from the experimental and control trees. These plugs included all the tissues from the outer bark to the surface of the xylem tissue and were removed from the tree with a 1 cm diameter grommet punch. Two plug replicates were collected from within 1 cm of the top holes of each sap well. I compared the percent moisture of the tissue samples between covered and uncovered treatments with a Wilcoxon matched-pairs signed-ranks test. Because I was testing the effect of repeated wounding with this experiment, I analyzed only those experimental pairs that had more new holes in the uncovered than covered wells at the end of the experiment.

Three types of controls were used in this experiment. One was a control for the effect of repeated wounding by sapsuckers. Each covered sap well had a matched uncovered well that was not wounded by the birds during the experiment. A second was a control for the

effect of tar-paper coverings on bark moisture. It was run by collecting bark plugs from the bottom of each sap well in an area that was covered by tar paper on the trees in the covered treatment and not covered in the control wells. Bark plugs were collected in the same manner as described above. This allowed me to compare bark moisture between areas of tree trunks covered with tar paper and those not covered without the possible influence of a difference in the number of wounds below each sample location on the trunk. A third control involved the comparison of bark moisture at breast height on each tree to confirm that there were no inherent differences in the individual trees before new attack by the birds. A paired design was used on all controls and Wilcoxon matched-pairs signed-ranks tests were used for the data analysis.

#### Construction of Artificial Sap Wells

In addition to the experiment with natural wells, I selected seven birch trees and constructed artificial sap wells by repeated wounding throughout the breeding season. During a 44 d period I drilled a combination of 5, 6, and 9 mm holes in a pattern of vertical lines similar to what sapsuckers make. I added 10-15 new holes approximately every 4 d to each well during this period. At the end of the experiment I removed bark and phloem tissue samples with the 1 cm grommet punch (as described above) to test for changes in moisture levels resulting from repeated wounding. Plug samples were taken within 1 cm of the top holes and 20 cm above the top holes in the artificial well on the bole of the each tree. Moisture levels between the plugs at the top of the wells and ones from 20 cm above the wells were compared with a Wilcoxon matched-pairs signed-ranks test (Siegel 1959).

#### Results

Daily observations of four sap wells that were not a part of the cover experiment revealed several interesting details of the sapsuckers' wounding techniques. Sapsuckers added new holes to existing wells immediately above old holes within 1-2 mm of the top of a previous hole (Fig. 4-1). New holes were started as small round openings through the bark and

phloem tissue to the surface of the xylem and then were enlarged by successive cuts into fresh tissue at the sides and above the wound. Holes were enlarged for several days in a row and sap could be collected from each individual hole an average of 3.1 d ( $\pm 1.8$ ,  $N=51$  holes) before sap flow ceased. New holes were added to sap wells each day. Thus, as the season progressed, each sap well increased in size as sapsuckers expanded vertical lines of holes up the tree's bole with only the topmost holes actually producing sap at any given time (Fig. 4-1). Sap wells differed in the number of new holes that were added per day (Table 4-1) (Kruskal-Wallis,  $df=3$ ,  $H=20.673$ ,  $p=0.001$ ).

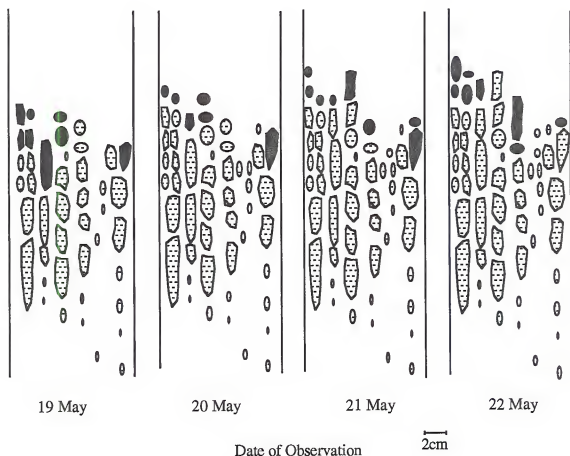


Figure 4-1. Changes in a sap well over four days in May 1993. Darkened holes designate those with sap flow, stippled holes have dried and no longer flow with sap. Note how new holes are added above older holes.

Table 4-1. The mean ( $\pm$ s.d.) number of new holes added per day in each of four sap wells.

SAP WELL	MEAN NUMBER NEW HOLES/DAY	N(d)
Aspen 1	5.7 $\pm$ 2.8	17
Aspen 2	2.0 $\pm$ 1.0	7
Juneberry	20.0 $\pm$ 5.9	5
Birch	5.9 $\pm$ 1.9	8

Moisture levels in bark and phloem tissue increased an average of 7.34 % ( $\pm$ 2.52) in sap wells that had been repeatedly wounded by sapsuckers over those that were excluded from the birds' use (Wilcoxon matched pairs signed-rank test,  $p=0.024$ ,  $N=14$ ) (Fig. 4-2). This increase was not a result of the tar paper covering (Wilcoxon matched-pairs signed-ranks test,  $p=0.4691$ ,  $N=16$ ) or bark moisture at breast height of the individual trees that were included in the experimental treatment (Wilcoxon matched-pairs signed-ranks test,  $p=0.8613$ ,  $N=13$ ). Artificial wells that I made by the repeated addition of new holes to artificial sap wells increased the moisture content of the bark and phloem tissue by 4.1 % ( $\pm$ 2.3) at the site of wounding (Wilcoxon matched-pairs signed ranks test,  $p=0.06$ ,  $N=7$ ) (Fig. 4-3).

When sap flow rates and sugar content of sap from active sap wells were compared to the cumulative number of new holes in each of four major sap wells, flow rates increased in three of the four wells but sugar content decreased with the addition of new holes in all four wells (Fig. 4-4). Taken together, however, this resulted in a net gain of total sugar flow per minute in three of the four wells as new holes were added throughout the breeding season.

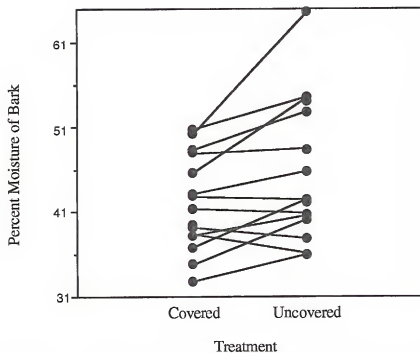


Figure 4-2. A paired comparison of moisture content of bark and phloem tissue in trees that sapsuckers continuously wounded during the breeding season (uncovered) and in trees that the birds were prevented from using (covered).

### Discussion

The patterns of moisture content in tissues of the trees changed after they were attacked by yellow-bellied sapsuckers. My attempt to create artificial sap wells suggested that repeated wounding with vertical lines of holes similar in size to sapsucker holes can increase the bark moisture above these incisions. These results suggest that sapsuckers increase their chances of successful phloem sap extraction with a repeated wounding technique.

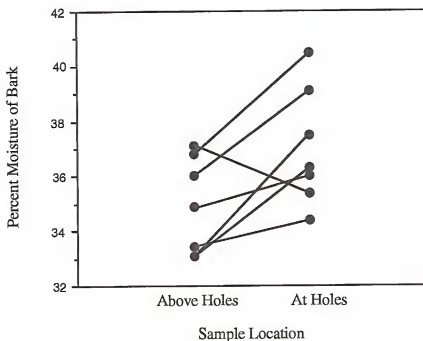


Figure 4-3. Moisture content of bark and phloem tissue within 1 cm of the top of seven artificially constructed sap wells and 20 cm above each artificial well.

My observations of active sap wells through time showed that sap flow from three of four wells was positively correlated with the cumulative number of holes added to each well. One surprising result was that at the same time the sap flow increased, sugar content decreased with repeated wounding through time in all the wells. Sugar content can decline naturally over time in phloem sap (Hill 1962). Because I was unable to measure sugar content of the sap of experimental trees due to the failure of my incisions to exude sap, I could not ascertain whether the decrease in sugar was due to a seasonal change in sap characteristics or an effect of the birds' activities. However, even though the sugar concentration of fresh sap samples decreased, sap flow increased and the result was that total sugar flow per unit time from each tree increased. Although fresh sap is more dilute, sapsuckers can take advantage of this increased flow of sugar by allowing fresh sap to

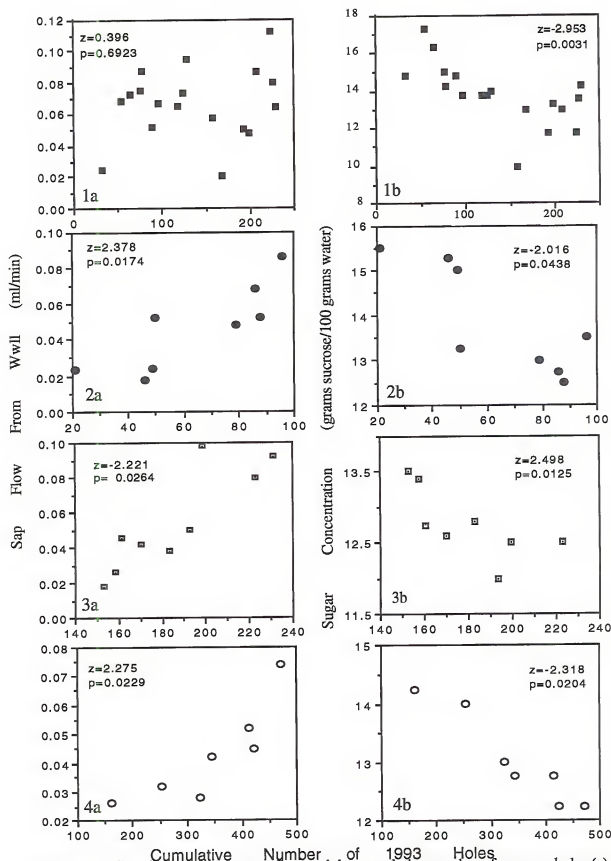


Figure 4-4. Correlations between sap flow and the cumulative number of new sap holes (a), and sugar content and the cumulative number of new sap holes (b) in four sap wells.



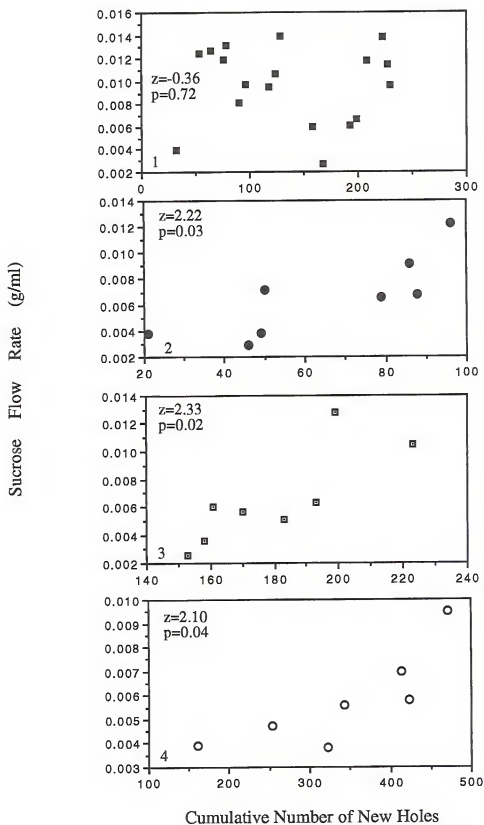


Figure 4-5. Correlations between sucrose flow rates and the cumulative number of new sap holes four sap wells flow (rates are calculated from information in Fig. 4-4).

evaporate, thus concentrating the available sugar (Kilham 1964). Sapsuckers appear to lick the surface of the bark below their active sap holes where evaporated sap may have collected (pers. ob.). Thus, the birds may increase sap flow from wells to compensate for a naturally occurring seasonal reduction in sugar concentration of phloem sap. Alternatively, they may wound trees to get more sap at the cost of obtaining more dilute sap. Either way they manage to obtain more total sugar from sap wells, probably as a result of their repeated wounding.

My data suggest that sapsuckers cultivate their sap food resource. Cultivation of a food resource has been observed in a wide variety of organisms including insects (Wheeler 1907, Way 1963, Quinlan and Cherrett 1979, Kleinfeldt 1986, Buckley 1987, Dorow and Maschwitz 1990, Devries 1991) and vertebrates (Clarke 1970, Sikkell 1989). Cultivation to obtain food differs in important ways from normal exploitation of resources because much energy and time are needed to make the resource available. A cultivated resource becomes more valuable through time if starting a fresh source of food is more costly than continuing to manage a current source. Strong territoriality is expected in such a system because the benefits of defending the large investment that is locked up in a valuable food resource will outweigh the costs of defense or of starting the cultivation process anew to obtain more food. A sap well that has been carefully farmed throughout the breeding season would be extremely important to protect from neighboring sapsuckers. Hadow (1977) found that two species of sapsuckers (*S. thyroideus* and *S. nuchalis*) nested farther apart from each other than they did from other cavity-building woodpeckers suggesting that competition for cavities is less important than defending food resources. In addition, sapsuckers increase their territorial behavior at the end of the breeding season when sap wells are used by both fledglings and adults but nesting cavities are no longer needed (Lawrence 1967). This also implies that territories are important for protecting access to feeding areas.

In my examination of sap wells, I was only able to test for flow rate and amount of sugar in the sap. Another measure of sap quality that may be important is its protein content

because protein is often a limiting nutrient for phloem-feeding animals (Raven 1983). Dying or stressed trees often have higher levels of amino acids in their phloem sap than healthy trees (White 1984). As noted in chapter 3, sapsuckers may prefer to attack dying trees for their sap. In addition, repeated wounding such as that done by sapsuckers could increase stress and induce a release of proteins into the phloem sap. In an analogous technique, a bruising method called cinching has been used by orchard growers to stimulate fruit production (Owen and Weigert 1982, White 1984). Thus, sapsuckers may repeatedly wound one or a few trees to increase protein availability in addition to increase sap flow.

In conclusion, yellow-bellied sapsuckers appear to cultivate their sap resource by repeated wounding in the form of clusters of sap holes on tree boles. This behavior has interesting implications for the benefits of defending a resource and may help to explain some of the observed patterns in territoriality in sapsuckers. In the next chapter I will address the possibility that sapsuckers may use saliva to stimulate sap flow from their sap holes. However, more research is needed that addresses what the sapsuckers' repeated wounding actually does to a tree's phloem sap and whether sapsuckers are able to compensate for diluted sap by waiting for natural evaporation to concentrate sap sugars.

## CHAPTER 5:

### THE POSSIBLE USE OF SALIVA BY YELLOW-BELLIED SAPSUCKERS TO STIMULATE PHLOEM SAP FLOW

#### Introduction

Many animals that eat transport fluids of both plants and other animals use saliva to facilitate the flow of these fluids from wounds. Blood-feeding arthropods employ saliva to help locate blood vessels in the skin of their hosts by disrupting the vessels and stimulating blood flow to create small hematomas that are easier to find than tiny vessels (see Ribeiro 1987 for review). Vampire bat (*Desmodus rotundus*) saliva contains anti-platelet activity that helps to stimulate the flow of blood from incisions cut into host skin (Hawkey 1967). Hookworms appear to have a similar ability to prevent the clogging of host blood (Eiff 1966). The saliva of leeches acts as an anticoagulant in the incisions they make for blood extraction (Muser et al. 1984). Like blood in animals, plant sap is protected by quick-sealing properties that prevent the loss of valuable transport fluids (see chapter 2). A variety of homopteran insects that feed on plant sap use saliva to unblock clogged sap cells and keep sap flowing from wounds (Bachus 1985, Dixon 1975, Risebrow and Dixon 1987). The evolution of specializations in salivary gland function for feeding on transport fluids appears to be widespread among blood and possibly sap feeders.

Animals that make incisions into phloem tissue and extract sap face the difficult problem of overcoming the plant's ability to prevent sap flow from such wounds (see chapter 2). Some animals that cut into phloem may have evolved ways of using saliva to stimulate sap flow and can therefore take advantage of the phloem sap as a food resource. Mackowski (1988) observed that yellow-bellied gliders lick the V-shaped incisions they make to extract

sap. When he found that similar artificial incisions did not exude sap, Mackowski suggested that these gliders may use saliva to stimulate the flow of sap.

During my research with yellow-bellied sapsuckers, I had very little success obtaining sap from artificial holes made in a variety of ways and in many kinds of trees (see Chapter 3). These included artificial wells I constructed that increased the moisture content of bark above them (chapter 4). This suggests that sapsuckers must employ some other mechanism, like saliva, to aid in phloem sap extraction in addition to selection of individual trees, repeated cuts into fresh tissue, and girdling (see previous chapters). The only situation in which I found sap flowing from my own incisions was when I made holes 1-2 mm above an active sapsucker hole where sapsuckers were frequently feeding. After making such cuts, sap would not immediately flow but when I returned 2-3 h later sap was flowing from such holes. The fact that my only successful holes were very close to active sapsuckers holes may not have been a coincidence. In those intervening few hours, sapsuckers may have processed my hole with their saliva to induce sap flow, or sap flow from my hole may have been a result of the processing of nearby holes.

If the saliva is used for sap extraction, sapsuckers may have had an evolutionary precursor leading to this adaptation in the form of modified salivary glands. The Picidae is one of only three groups of birds with modified salivary glands (McLelland 1979). An enlarged portion of the mandibular glands fills the space between the rami of the mandibles in woodpeckers. In insectivorous species these glands produce copious amounts of sticky saliva on the tongue that aids in pulling insects from crevices in wood (McLelland 1979). Thus, it is likely that the ancestors of sapsuckers had a serendipitous preadaptation to facilitate the evolution of the use of saliva as an aid in sap-extraction behavior.

In this chapter, I test the hypothesis that sapsuckers can keep sap flowing from their holes by a continual processing of their bark incisions, and I explore the possibility that saliva is an important factor in their success at sap extraction. To accomplish this I performed a hole-cage experiment in which I predicted that an uncaged sap hole to which

birds had access would continue to flow with sap longer than a caged hole from which birds were excluded. In addition I predicted that if sapsuckers use saliva, a positive result in the hole-cage experiment would not be a consequence of continued enlargement of holes or continued removal of sap from those holes. I also made observations of holes in sap wells and observed the feeding behavior of sapsuckers to look for evidence that sapsuckers may add saliva as they process sap holes.

### Methods

In May-July 1993 I repeatedly visited four active sap wells maintained by three pairs of sapsuckers. I define an 'active sap well' as having sap flowing from at least one hole. These four wells were located in one paper birch (*Betula papyrifera*), one juneberry (*Amelanchier* spp.) and two big-toothed aspen (*Populus grandidentata*). The two aspens were used by the same pair of birds while the birch and juneberry were each constructed by separate pairs of sapsuckers. All four trees were located on the property of the University of Michigan Biological Station in Cheboygan County.

During my observations I marked individual sap holes with waterproof ink, measured their length and width, and noted if they had sap flowing from them. Length and width were measured with a 15 cm plastic ruler laid across the top of each hole and were defined as the vertical and horizontal distance between the cut edges of the outer surface of the bark. In the case of irregularly shaped holes the maximum possible distances were used. Holes exuding fresh sap were called 'open' holes. Dry holes or those with sap flow blocked were called 'closed' holes. By returning on subsequent days, I could determine when the birds started new holes, how much they enlarged holes each day, how many new holes they constructed each day, and the length of time each hole exuded sap. I measured the flow rate of sap by evacuating holes with a tuberculin syringe and collecting and measuring all of the fresh sap that exuded after a timed interval. The sucrose concentration of the sap was

determined with a American Optical T/C hand refractometer model 10431 (see Chapter 1 for details).

I obtained the feeding rate of sapsuckers by observing them with binoculars at a distance of 10-50 m. No blind was used for these observations because I could find patches of vegetation or tree trunks for concealment. For more detailed observations of their hole-visiting behavior, I constructed a blind 6 m high in a tree that was 5 m from an active sap well. This allowed me to observe sapsuckers at their sap well without causing excessive disturbance.

I performed a cage experiment to test whether the sapsuckers could keep holes open by their activities at the sap wells. I used a paired design in which I matched open holes for size, age, and proximity on the same tree. Before I set up the experiment I measured the length and width of both holes and collected sap from each with a sterile syringe. One of each pair, chosen randomly, was covered with a new, unused piece of rectangular aluminum window screen creased along its long dimension to form a tent-shaped cage. These cages were fastened over the holes with metal tacks at the sides. The cages allowed air to flow over the holes and insects to access the sap but they excluded sapsuckers and other vertebrates from using the caged holes. The remaining hole was left uncaged. I returned to check on the fate of the holes within 24 h. I continued to monitor the holes until at least one of the pair had closed. I then removed the screen and tacks and remeasured both holes.

In a test of the effect of the repeated removal of sap from holes I used a double-cage experiment. For this test I matched sets of three holes for size, age, and proximity to each other in the sap well. I then caged two of the three holes with screen. At intervals which approximately matched the visitation rate of the sapsuckers at their sap well, I removed sap from one of the two caged holes with a sterile syringe. Sap evacuations were made between the time of set up (10:00-11:00) and dusk of that day. No sap evacuations were made on subsequent days. I followed the fate of all three holes until at least two of the holes had

closed, checking them at least every 24 h. I repeated this double-cage experiment three times using three different sap wells on three different sapsuckers territories.

### Results

A typical hole in the bark made for phloem-sap collection was shaped with undercuts into the bark on the sides and cuts that were perpendicular to the surface of the xylem tissue at the top and bottom, resulting in a flat surface or shelf along the bottom of the hole (Fig. 5-1). Sap collected on this bottom shelf as it oozed from the top and sides of the hole. Despite the fact that sap collected on the bottom shelf of each hole, sap often overflowed from such holes and dripped down the bark below the active hole. Sap holes that were active varied in size depending on individual sap wells (length: ANOVA,  $F_{3,487}=11.688$ ,  $p=0.0001$ , width: ANOVA,  $F_{3,487}=4.775$ ,  $p=0.0027$ ) (Table 5-1). All holes in all wells ranged in size from 2 x 4 mm to 17 x 23 mm.

Table 5-1. Mean ( $\pm$ s.d.) length and width of active holes in each of four sap wells.

SAP WELL	N	AVERAGE LENGTH (mm)	AVERAGE WIDTH (mm)
Aspen a	253	6.8 $\pm$ 3.2	10.5 $\pm$ 2.4
Aspen b	61	8.1 $\pm$ 4.0	10.4 $\pm$ 3.3
Birch	109	6.3 $\pm$ 3.3	10.2 $\pm$ 2.4
Juneberry	68	9.3 $\pm$ 5.4	11.8 $\pm$ 4.8

When visiting these phloem sap holes, sapsuckers made a characteristic pattern of movements while processing each hole. Birds would lap with their tongue the inner surface where the bark met the xylem tissue of both sides as well as the top edge of the hole. In addition they would also dip the tip of the bill into the large drop of sap that had collected at



the bottom of the hole (N=21). The bill was held slightly agape during all of these procedures.

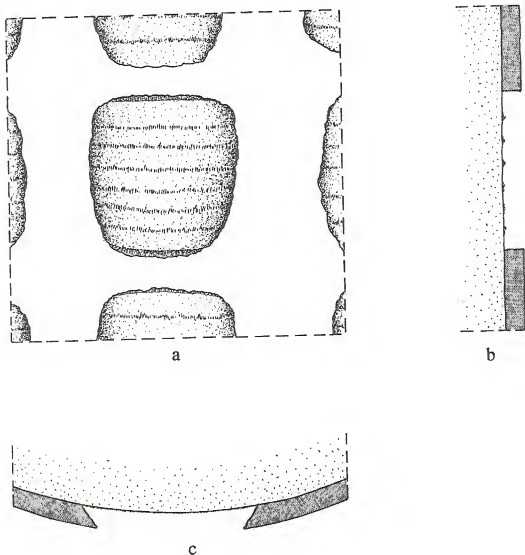


Figure 5-1. Representations of a typical completed sap hole cut in the bark for phloem sap extraction. Frontal view (a) shows faint lines left from successive enlargements. A longitudinal section (b) reveals that the top and bottom edges are cut perpendicular to the surface of the xylem tissue. A cross section (c) shows that the sides are made at an acute angle to the back surface of the hole. Gray areas on longitudinal and cross sections denote the bark of the tree.

I observed sapsuckers performing this hole processing on every open sap hole in a well at least once during each visit (N=8). In one case a male visited each active hole at least five times in one visit. Birds visited sap wells an average of 5.25 times per hour ( $\pm 2.77$ , N=4

birds) in early and mid-May, and in mid-June I observed a visitation rate of 5.5 times per hour ( $\pm 0.5$ ,  $N=2$  birds)

In the caged-hole experiment, birds never hesitated to approach uncaged holes and use them even when cages had been placed on adjacent holes. One cage was disturbed during the experiment by squirrel interference and that replicate was lost. In the other 16 replicates, caged holes closed before uncaged holes or they both closed at the same time (sign test,  $x=0$ ,  $n=13$ ,  $p=0.001$ ). Holes were watched until at least one of each pair had closed and this time to closing ranged from 11 to 72 h.

Two very different situations led to closure of holes. Three of the 19 holes that I saw close during the experiment simply dried out. The other 16 holes closed when a thickened white substance of unknown origin appeared to block sap flow. A yeasty smell accompanied most of these holes. The thickened white substance ranged from yellowish, opaque, and bubbly to white, translucent, and gel-like. In one caged hole, I removed the thickened white substance that had formed during the experiment and left the hole uncaged for the birds' use but sap did not begin to flow again from this hole.

The 17 sap holes that remained uncaged had an average length of 5.4 mm ( $\pm 3.7$ ) and width of 9.9 mm ( $\pm 3.2$ ) at the start of the experiment. Birds enlarged some of these uncaged holes during the experiment. Of 12 uncaged holes that remained open, seven had been enlarged while five remained the same size as when I started the experiment. In the seven that were enlarged, holes were lengthened only from the top of the hole by an average of 2.9 mm ( $\pm 1.2$ ) and widened by an average of 1.4 mm ( $\pm 1.7$ ).

In all three replicates of the double-cage experiment, the evacuated hole did not remain open longer than the caged, undisturbed hole. In two of the three replicates the third hole that was left available for the birds to use remained open longer than the two caged holes.

### Discussion

The results of my hole cage experiment show that sapsuckers maintain the flow of sap in sap holes that they use. I found that only about half of uncaged holes that remained open longer than caged holes were enlarged by the birds during the experiment. The other holes continued to flow with fresh sap from the surface of old incisions without further enlargement. Thus, it was not likely that the birds kept their sap holes open solely by continued enlargement of holes and creation of fresh incisions made in undisturbed phloem cells above and to the side of holes. In addition, I found no evidence to suggest that the constant removal of sap from sap holes could keep sap flowing from holes and prevent drying or blockage. Therefore, I suggest that sapsuckers have some other method to open and maintain holes such as saliva or mechanical abrasion with the tongue.

I observed sapsuckers licking the sides and top surface of the incisions around their sap holes. This may have been a way for them to collect sap that oozed from these incisions. In addition, it also may serve to deliver saliva to the cut surface of the phloem tissue or to abrade the cut surface. Sapsucker tongues have a soft consistency with a fine brushy border (Zusi and Marshall 1970). The amount of abrasion necessary to make and maintain several sap holes at one time and continuously throughout the year makes it unlikely that they could keep sap flowing by tongue abrasion. Thus, the use of saliva appears to be a more likely hypothesis for why uncaged holes remain open given the information available.

The brushy border that is characteristic of the tongues of sapsuckers has been assumed to function in picking up the sap that has oozed from incisions (McAtee 1911). However, the protrusions on the edge of the tongue could serve to transport saliva out of the mouth and direct it to the cut surface of phloem cells. I observed sapsuckers collecting sap from the large droplets of fluid that collected in the bottom of active sap holes by dipping their slightly agape bill into the liquid. During this type of sap collection the tip of the bill was held lower than the base suggesting that the sap travelled up the bill against gravity. This is reminiscent of the way plankton-feeding phalaropes feed by taking advantage of the

adhesive qualities of a long, absorbant beak (Rubega and Obst 1993). Perhaps sapsuckers can collect sap without the need for a brushy tongue but cannot deliver saliva to sap holes without this specialized morphology.

The results of my cage experiment suggest two possible actions of saliva in sap holes. As suggested in the introduction, sapsuckers may be able to use their saliva to prevent or remove the p-proteins and callose that clog the sieve pores in the phloem tissue upon injury in a manner similar to aphids (Salisbury and Ross 1992). Evidence suggest that adjacent, intact cells in the sieve tubes do not become blocked when sap flow is disrupted, because new incisions only a short distance away from clogged tissue flow with sap for a short time (Crafts and Crisp 1971). Thus, is enzymes in saliva can clear protein or callose blockages in the sieve plates at an incision, sap flow may be restored in the sieve tubes. Such an anticoagulant function would be analogous to the use of saliva by blood-feeding animals to prevent clots during blood extraction. Another possibility is that saliva prevents the formation of a gum-like exudate that may be produced by the tree as an alternate way to prevent the loss of phloem sap. Thus, the saliva of these birds may interfere with the tree's protective abilities in more than one way.

In addition, sap flow was arrested in many holes in my experiment by the formation of thickened white substance that smelled strongly of yeast. Thus, some of the blockages were likely a byproduct of a microbial infection in the sap holes. Perhaps the microbes lived on the sugars in the sap and eventually blocked the sapsucker holes. In the blocked holes that did not have a distinctive yeasty smell, the infection may have been bacterial with the same end result. Such microbial infections may cause the formation of alcohols in the sap holes, because sapsuckers have been observed acting as if they were under the influence of alcohol (Bent 1939). Saliva from other organisms has been shown to have antimicrobial properties (Gambino 1993) and sapsucker saliva may also have such a function. Thus, saliva may serve the dual purpose of preventing the blockage of sap flow as well as preventing the formation of alcohol buildup in the sap holes. In summary, sapsucker saliva may function

to keep holes open by acting as an antimicrobial agent that prevents infection in sap holes or as an anticoagulant that can stop the formation of exudate or clear clogs in the phloem tissue.

If sapsuckers use saliva to extract sap from trees as my evidence suggests, this would be one of the first reported cases of such an adaptation in any sap-eating vertebrate. Many questions remain about this unusual phenomenon including how the saliva glands of sapsuckers compare to those of other woodpeckers. One puzzle that remains is why other species of woodpeckers that are able to peck through bark do not extract sap from trees, but rather steal it from sapsuckers (Foster and Tate 1966). Further, comparisons are needed between sapsuckers and the other species of woodpeckers that apparently eat phloem sap such as acorn woodpeckers and rufus-bellied woodpeckers, to explore whether the use of saliva is an adaptation typical of other sap-extracting birds and whether they have saliva with antimicrobial agents or anticoagulant properties. Finally, this study raises a whole new set of questions about the chemical properties of sapsucker saliva and its possible action as an anticoagulant or antimicrobial agent.

## CHAPTER 6:

### FACTORS AFFECTING REPRODUCTIVE SUCCESS IN YELLOW-BELLIED SAPSUCKERS

#### Introduction

#### Overview

Knowledge of the factors influencing an individual's fitness can lead to a better understanding of the evolution of specific behavioral adaptations (see Clutton-Brock 1988 for review). Fitness differences include variation in reproductive success and are the basis of natural selection (Endler 1986). In this chapter I explore three correlates of variation in reproductive success of yellow-bellied sapsuckers: 1) the supply of food available, 2) the availability of nest sites, and 3) the prior breeding experience of parents. All three of these involve the supply of resources or the ability to garner them. With this information, I suggest the current selective pressures that may be acting on these woodpeckers and speculate on what selective pressures may have acted in the past to shape the special characteristics of this species, which is unusual among woodpeckers.

#### Food Supply

The supply of food can limit reproductive success if offspring are unable to get the nourishment they need to survive and grow (Clutton-Brock 1988). In an altricial bird, such as the sapsucker, nestling health and survival depend on the male and female parents' ability to deliver good quality food in large quantities to the growing chicks in the nest cavity. Sapsuckers feed their chicks a mixture of arthropods, phloem sap from trees, and fruit (Tate 1973). Individuals that are able to defend better territories with more foraging sites might have a higher reproductive success. I will test the hypothesis that access to food resources

is a limiting factor to reproductive success for yellow-bellied sapsuckers by measuring how sap and arthropod abundance correlate with measures of breeding success in these birds.

### Nest Sites

Nest sites are known to be a limiting factor of woodpecker populations in general (Peterson and Grubb 1983, Welsh and Capen 1992). Thus, the availability of nesting sites may contribute to the variation in reproductive success of sapsuckers. Like other woodpeckers, yellow-bellied sapsuckers are primary cavity nesters and usually build a new nesting cavity for each breeding attempt (Kilham 1962a, Kilham 1977). Nesting cavities are most often constructed in living aspen trees that have been infected with the fungus Fomes igniarius var. populinus (Shigo and Kilham 1968, Kilham 1971). Preference for such specific, infected trees, indicates other uninfected trees may be unsuitable and sapsuckers may be forced to reuse old holes because no appropriate trees are available. Such re-use may result in reduced nest success from parasites present in old nests. I will examine the hypothesis that the ability to obtain and construct a nest cavity contributes to variation in breeding success. To address this hypothesis, I will compare the success of sapsuckers that build new cavities with those that reuse old cavities and in addition look at how the number of cavities started by each pair is related to breeding success.

### Breeding Experience

Age of breeding adults can be an important influence on breeding success (Newton 1988). Older individuals may be able to acquire better territories, defend them more effectively, and provide better care for offspring. In many of my tests for resource limitations, I assume that resources may be limited because they are in short supply and individuals that are better able to garner them, because of age or other factors, are more successful. In addition, older individuals often produce bigger clutches and can raise more successful offspring in one breeding attempt (McCleery and Perrins 1988), not because they have better resources available to them but because they are more efficient care-givers. This could also be true of sapsuckers. In a marked population of sapsuckers in southern

Ontario, Lawrence (1967) had one male return to breed six times and others that returned two years in a row. These returning sapsuckers used the same territories in their successive breeding attempts, suggesting that older age and the experience that accompanies it could influence breeding success in yellow-bellied sapsuckers.

In addition to addressing the effects of access to resources and age on breeding success, I also consider predation as a factor influencing reproduction. The ability to avoid predation is a major factor that influences reproductive success in some species (Fitzpatrick and Woolfenden 1988). Nestling sapsuckers remain in the nest cavity from 25-29 d (Jackson 1976) and are vulnerable to predators that are able to enter or reach into the nest. Sapsucker nests have been attacked by red squirrels, Tamiasciurus hudsonicus (Lawrence 1967), weasels, Mustela spp. (Johnson 1947), and black bears, Ursus americanus (Franzreb and Higgins 1975). I will explore the importance of predation pressure to sapsucker reproductive success by observing the level of predation on both adults and nestlings.

## Methods

### General Methods

During the 1991, 1992, and 1993 breeding seasons, I studied the breeding behavior of yellow-bellied sapsuckers at the University of Michigan Biological Station, Cheboygan County (see Chapter 1 for full description). Active sapsucker nests were located by listening for the sounds of excavation, observing the behavior of adults, and by listening for the sounds of begging from chicks in the nest. Some nests were located earlier in the breeding cycle than others, and thus complete sets of data are available for only a subset of the total number of nests that were located. In addition, a Swedish climbing ladder was used to reach as many cavities as possible. However, nests in crooked or weak trees could not be reached for some portions of data collection.

I used three major categories of characteristics as measures of reproductive success for these sapsuckers. These include parental effort, development time, and number of



offspring. I will describe each of these dependent variables in detail below and then address how I measured the independent variables of food availability, nest site availability, and age.

Parental effort was measured by observing the number of feeding visits that parents made to the nest at two different times during the breeding cycle. Early-season watches were made when the chicks were approximately 7 d old. I made late-season watches at approximately 21 d of age. For each watch, I sat quietly on the forest floor 10-50 m from the nest tree for 15 min before beginning observations. I recorded the number of visits by adults with food for a one hour period.

I calculated development time by observing the hatching and fledging dates of each nest. Hatching dates were determined by looking into the nest and estimating nestling age or by using the behavior patterns of the adults at the nest (Jackson 1976). Before hatching, adults spent long bouts (>20 min) in the cavity but after hatching the length of time spent in the nest lessened and adults could be observed carrying food to the chicks. Fledging time was determined to the nearest day by visiting a nest each day just before expected fledging and listening for the begging calls of nestlings still in the nest.

Offspring number was determined in several ways at two stages of the breeding cycle. At approximately nine days after hatching, I climbed up to each nest cavity and captured as many nestlings as possible from the nest entrance with a monofilament noose (as described by Jackson 1982). I weighed each nestling with a 50 g Pesola spring scale and banded it before returning it to the nest cavity. There was no abandonment after this procedure. Within one week of fledging, I again climbed to every nest and counted the total number of nestlings in the cavity using a small battery-powered reading light and angled mirror on a stick. I defined this number as the fledging number of chicks and subtracted the number at the nine-day-old noosing from number at fledging to obtain a value for chick loss. A nest was defined as attacked by predators if all nestlings disappeared suddenly without other explanation or if I discovered the remains of sapsuckers in or below the nest. Cavities that

experienced predation were included in analyses and in all but one case resulted in a fledging number of zero.

### Food Availability

I tested how two different aspects of food availability influenced reproductive success. First, I conducted a field experiment to test whether the number of old sap wells from previous years in living trees influenced breeding success in the current year. Second, I examined the variation in arthropod abundance between territories and hypothesized that territories with more arthropods would have higher success. Below I will describe in detail the methods for testing these two hypotheses.

Long-term value of old sap wells. Yellow-bellied sapsuckers extract sap from the same trees in successive years and old sap holes were clearly visible for several years after they were first active. In this experiment, I defined major sap wells as those that contained 100 or more old holes (see Chapter 4 for description of sap well). As returning adult sapsuckers established territories in the area, I counted the number of old sap wells on each territory. Old sap wells were easily located early in the season when deciduous forest trees were devoid of new leaves. I then set up an experiment using a matched-pair design to test for the effect of the availability of old sap wells on reproductive success. Territories were matched by nest completion date. This procedure helped to minimize variation in individual bird quality within matched territories.

I randomly selected one of each of these matched pairs of territories and covered one half of the old sap wells in that territory to prevent the use of these old wells by the breeding sapsuckers. I used the Swedish Climbing ladder to reach old sap wells. Although I attempted to choose trees for covering at random, I was unable to reach some of the old sap wells by free climb or with the ladder and covered lower wells instead. Covers consisted of two layers of material. The first was a piece of galvanized hardware cloth (mesh size = 4mm) nailed to the tree trunk at the top of the sap well with galvanized roofing nails. Over this I nailed a layer of tar paper that was painted on the outside surface with white paint in a

way that mimicked the bark of the host tree. Thus the completed cover made location of the old sap well visually difficult and access to the well impossible for the sapsuckers. After the experiment was completed, the covers were removed and access to the wells restored.

Control territories were treated with a similar level of disturbance and tar paper covers were placed on undisturbed portions of the trunks of one half of their sap-well trees at least one meter below the old sap wells. A total of nine pairs of territories were treated in this way and all covers were in place by 3 June. Although it took about three weeks to install all the covers, experimental and control covers were placed on each matched pair of territories on the same day or in two consecutive days.

Between the time all the covers were in place and fledging or nest failure, I monitored all 18 territories for the three kinds of breeding-success variables described above. For parental effort data collection, paired experimental and control nests were observed on the same day within one hour of each other. In addition, I followed the fate of each major sap well and recorded whether sap flowed during the time of the experiment and whether major wells were built in fresh, undisturbed trunk or above old sap wells. Comparisons between experimental and control nests were made with Wilcoxon matched-pairs signed-ranks tests (Siegel 1959).

From previous observations (see Chapter 3), I expected that on control territories, most major wells would be constructed above old scars. However, on experimental territories, I expected that if the birds are limited by the presence of old sap wells for obtaining sap, I would find either a reduction in breeding success and/or an increase in the number of sap wells on fresh, undisturbed tree trunks.

Arthropod abundance. Also during the 1992 breeding season I surveyed arthropod abundance on each of 16 active sapsucker territories. Numbers of arthropods were counted on the surface of tree bark and on leaves and twigs in the understory. Preliminary observations in 1991 revealed that sapsuckers glean arthropods from both of these areas. Systematic surveys were made along two transects per territory that were laid using the nest

tree as a starting position and the two most active sap wells as determinants of direction. Thus each transect included a part of the territory with the highest sapsucker activity. Every ten paces along the transect I located the closest tree  $\leq 5$  cm circumference at breast height and the 20 closest red or sugar maple leaves between 0.5 and 2 m above the ground. On the trees I counted the number of arthropods on the surface of all bark between the ground and two meters high. On the 20 leaves and their corresponding twigs I counted all arthropods present. A total of ten trees and ten groups of leaves were used for estimates of arthropod abundance in each territory. Care was taken to separate arthropods into categories on both bark and leaves. Some of the forests around the University of Michigan Biological Station experienced severe gypsy moth attack during the summer of 1992. Because I never observed a sapsucker capture and eat a gypsy moth even when the moths were very abundant, I excluded gypsy moth larva from my analysis. Arthropods in this survey included mayflies (Ephemeroptera), caterpillars and adult butterflies and moths (Lepidoptera), beetles (Coleoptera), flies (Diptera), ants (Hymenoptera), aphids and scale insects (Homoptera), and spiders (Arachnida). Arthropod abundance was compared to the measures of reproductive success on each territory with a Spearman rank correlation.

#### Cavity Tree Availability

Kilham (1962a) noted that when yellow-bellied sapsuckers begin excavations of cavities in early May, they often start three or four different holes before settling on one for completion. Aborted holes that are started but not completed may represent trees that are not suitable for completing a cavity. Much time and effort goes into working on these aborted holes, and sapsuckers with excellent trees available for cavity construction may be able to avoid such a cost of time and energy. In 1992 I counted the number of hole starts made by each pair and compared it to the measures of reproductive success with a Spearman rank correlation

In addition, some pairs reused an old nest cavity rather than constructing a new cavity. I hypothesized that these pairs were unable to use a new cavity because their territory did not

contain appropriate trees or they did not have the skill to excavate a new one. I examined whether nesting in a new cavity could be an advantage by comparing the measurements of reproductive success from nests made in new cavities and those in reused cavities with a Mann-Whitney U test.

### Age

I compared the success of experienced birds with that of new breeders by following the fate of nests with at least one of the pair either a known returning adult or a known new breeder. In 1991 and 1992, I marked both adults and young with unique combinations of plastic colored leg bands. Adults were captured in mist nests by sap or nest trees or in clear plastic bags as they attempted to leave their nest cavities in the morning. Nestlings were noosed from cavities at approximately 8 d old and banded (see above). Returning birds were identified in 1992 and 1993 and their breeding success compared with Mann-Whitney U tests.

## Results

### General Reproductive Success

The overall average number of eggs laid in all nests was 5.44 (N=27 nests) and successfully fledged offspring was 2.72 (N=32 nests). The variance was higher for fledgling number ( $\pm 1.75$ ) than for eggs laid ( $\pm 1.19$ ). Clutches were reduced by one half on average between egg laying and fledging. Brood reduction appeared to be a result of a combination of unhatched eggs and disappearance of nestlings from the cavity. Egg shell, and unhatched eggs disappeared from the nest cavity within one day of hatching and I could not determine infertility rates in eggs. No evidence of predator invasion could be detected in the nests with missing eggs. In 1992, average chick loss for nestlings between 8 d and fledging was  $1.38 \pm 0.99$  (N=16). Average hatching to fledging time was  $26.9 \pm 1.38$  d (N=24). Average fledging date for all years was 4 July  $\pm 3.5$  d (N=31).

From three years of nesting data, I could not detect any differences between years for the number of eggs laid (Kruskal-Wallis,  $N=27$ ,  $P=0.49$ ). I also did not find differences between 1992 and 1993 in the number of successfully fledged young (Mann-Whitney U,  $n_1=16$ ,  $n_2=16$ ,  $p=0.38$ ) or fledging date (Mann-Whitney U,  $n_1=15$ ,  $n_2=12$ ,  $p=0.80$ ).

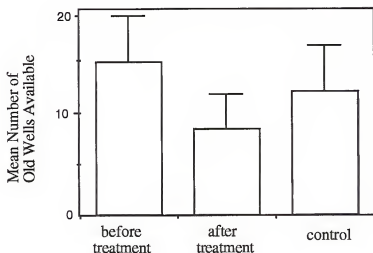


Figure 6-1. Number of old sapwells available to the birds on experimental and control territories at the start of the breeding season.

#### Food Availability

I successfully reduced the number of old sap wells available to the birds on the experimental territories with my covering treatment (Wilcoxon matched-pairs signed-ranks test,  $N=8$ ,  $p=0.0340$ ). (Fig. 6-1). However, the experimental and control territories in the old-sap-well experiment did not differ significantly in breeding success for the variables I measured (Table 6-1). At the end of the breeding season, there was no significant difference in the percentage of available old sap wells that had been used during the season between experimental and control groups (Table 6-1). Five out of seventeen major sap wells that had sap flow during the season were constructed on new, unused tree trunk with

no old-hole scars. However, only one of these five was on an experimental territory with covered wells. The rest were made on control territories where all original old sap wells remained open.

I found no significant relationship between the number arthropods available on a territory and hatching date, fledging date, hatching to fledging time, number of successfully fledged offspring, brood reduction, or feeding rates measured as a combination of early and late nesting cycle watches (Fig. 6-2).

Table 6-1. Comparison of mean ( $\pm$ s.d.) response results of the experiment to limit the number of old sap wells available.

VARIABLE	N	COVERED	UNCOVERED	P-VALUE
% Accessible old wells that were used	7	34.3 $\pm$ 18.5	53.8 $\pm$ 33.9	0.4460
<b>Parental efforts</b>				
number of feeding visits/h				
early season	8	12.4 $\pm$ 4.9	15.1 $\pm$ 4.9	0.6219
late season	8	20.6 $\pm$ 7.4	22.9 $\pm$ 6.1	0.4384
<b>Development time</b>				
hatch date	8	5.9 $\pm$ 2.7	8.4 $\pm$ 4.7	0.2053
fledge date	8	3.8 $\pm$ 3.8	5.1 $\pm$ 4.6	0.3991
hatch-fledge time	8	27.6 $\pm$ 2.1	25.8 $\pm$ 1.3	0.1308
<b>Breeding success</b>				
mass at 9 d	8	30.1 $\pm$ 7.5	29.4 $\pm$ 4.0	0.6744
number at 9 d	8	4.4 $\pm$ 0.9	4.5 $\pm$ 0.8	0.7855
number fledged	7	3.1 $\pm$ 1.2	3.1 $\pm$ 1.2	1.0000
brood reduction	8	1.5 $\pm$ 0.9	1.4 $\pm$ 0.9	0.7055

### Cavity Trees

I did not find a relationship between the number of hole starts and the number of young fledged, fledging date, hatching to fledging time, or feeding rate (Fig 6-3.). However, the number of cavities started correlated with hatching date (Fig. 6-3). I also found significant differences between birds nesting in new cavities and those that reused old cavities. Birds nesting in old cavities laid an average of 1.3 more eggs than pairs in new cavities (Mann-Whitney U test,  $p=0.024$ ), but tended to fledge about half the number of offspring as compared with pairs in new cavities (Mann-Whitney U  $p=0.079$ ) (Table 6-2). Other measures of reproductive success did not differ significantly between birds in new and reused cavities (Table 6-2). In contrast to newly made cavities at the start of the season, old cavities had a layer of black moist material in the bottom of the nest and in cavities where I was able to see clearly, I could detect the movement of arthropods in this material. Old cavities also had dark, moist walls in contrast to the clean, fresh, dry wood of new cavities.

Table 6-2. Mean ( $\pm$ s.d.) measures of reproductive success for newly constructed cavities and reused cavities. P-values resulting from Mann-Whitney U tests are given.

VARIABLE	Cavity Type				
	REUSED	N	NEW	N	P-VALUE
number of eggs	5.7 $\pm$ 1.2	5	4.4 $\pm$ 0.6	21	0.0237
number fledged	1.6 $\pm$ 1.5	7	3.0 $\pm$ 1.8	22	0.0787
no. eggs-no. fledged	3.2 $\pm$ 1.7	4	2.7 $\pm$ 1.8	19	0.3766
hatch-fledge time (d)	27.0 $\pm$ 0	2	26.8 $\pm$ 1.4	20	0.7246
fledging date	5 July ( $\pm$ 6.0)	5	4 July ( $\pm$ 3.1)	22	0.9749



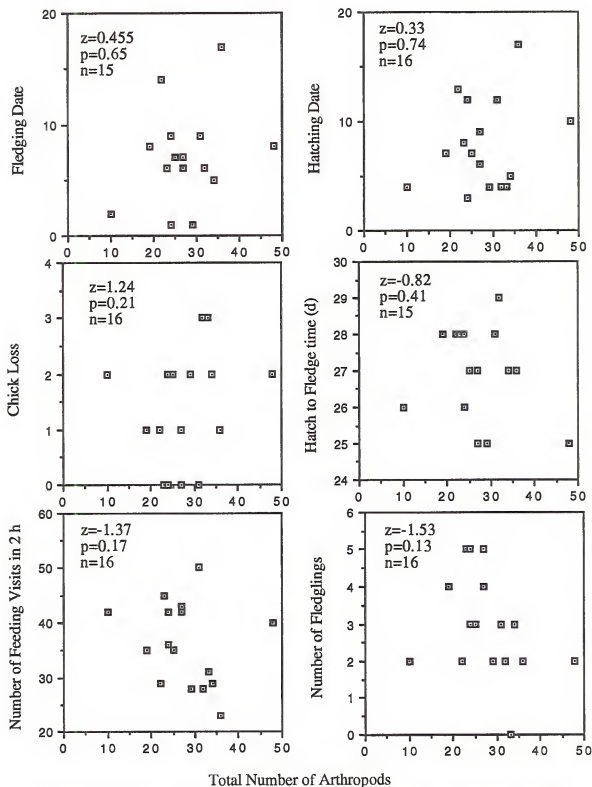


Figure 6-2. Correlations between the numbers of arthropods in standardized surveys and measures of reproductive success on each territory. Results of Spearman Rank Correlation Coefficients are given on each graph.

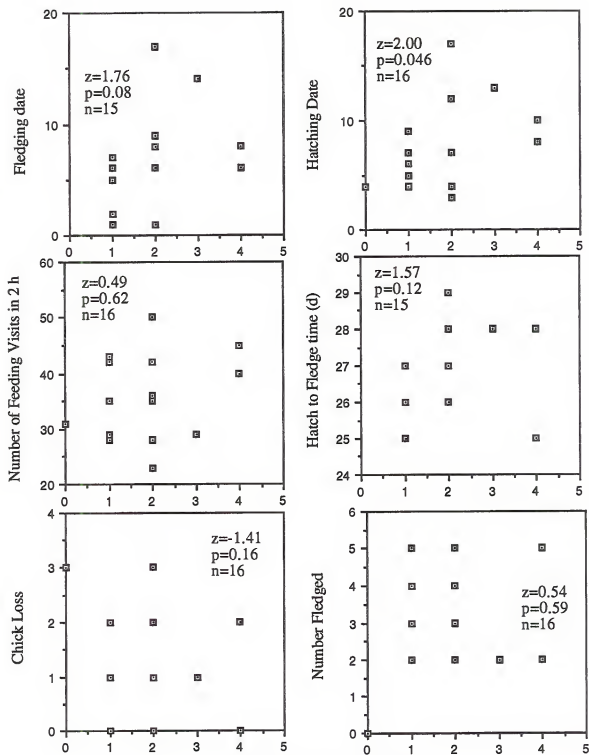


Figure 6-3. Correlations between the number of cavity starts made on each territory and measures of reproductive success. Results of Spearman Rank Correlation Coefficients are given on each graph.

### Age of breeders

Of 11 breeding birds in 1992 and 1993 of known age, 7 were breeding for at least the second time in their lives and 4 had fledged from nests in the area the previous year. In one case a returning adult and a young bird paired and the data from this pair were excluded from the analysis to avoid replication. In another case, two returning adults bred together and these were included as one data point for old birds. Of the remaining birds I did not know the history of any of their mates. I found no significant differences in the reproductive abilities between old and young birds in number of eggs laid, number fledged, hatching date, fledging date, or hatching to fledging time (Table 6-3). Data on parental effort were not available for enough of these birds for an analysis of the differences between experienced and new breeders.

Table 6-3. Mean ( $\pm$ s.d.) measures of reproductive success for sapsuckers breeding for the first time (new) and those with breeding experience (exper.). P-values resulting from Mann-Whitney U tests are given.

VARIABLE	Breeding Status				
	EXPER.	N	NEW	N	P-VALUE
number of eggs	6.2 $\pm$ 1.6	8	6.3 $\pm$ 1.2	3	0.8288
number fledged	1.5 $\pm$ 2.1	8	2.5 $\pm$ 1.9	4	0.4108
fledge date	5 July ( $\pm$ 1.4d)	2	3 July ( $\pm$ 2.5d)	3	0.5428
hatch date	6 June ( $\pm$ 4.4d)	5	6 June ( $\pm$ 0.7d)	2	0.6959
hatch-fledge time (d)	27.0 $\pm$ 1.4	2	28.5 $\pm$ 0.7	2	0.2207

### Predation

During three years of study and close watch of 39 nests, I found evidence that 8 of those nests were attacked by predators. Of the other nests, 30 successfully fledged young and

one did not appear to fledge young but I could find no evidence of a predator attack on the nest. I could determine the probable fate of 69 adult breeding birds during my study. Of these adults, only two disappeared during the period between nest initiation and fledging in possible predation events away from the nest cavity. At least three other adults were taken by predators at the nest cavity. Thus, predation levels for nestlings appeared to be higher than for breeding adults in my study. Although I witnessed one unsuccessful hawk attack on a female early in the season, all known successful predation on adults was on males. This hawk attack was the only predation attempt that I witnessed. In other predation events, I found feathers and body parts around the nest indicating that the predators were likely to be small mammals such as squirrels or weasels.

### Discussion

My experiment that excluded the use of old sap wells from some sapsuckers showed that the availability of old wells does not limit reproductive success in this area. My experimental treatment did not significantly influence any of the reproductive success variables that I measured and did not significantly alter the percentage of available old sap wells that the birds used on the experimental territories. This suggests that individual differences in reproductive success are influenced by factors other than their ability to access old sap wells. In another aspect of this study (see Chapter 3), I found that sapsuckers may cultivate their sap resource during the breeding season. Future research should address the possibility that the total number of cultivated sap wells or the total sap flow per territory may influence variation in breeding success.

I also found no significant correlations between my measure of arthropod abundance and the variation in reproductive success that I measured. Arthropod abundance was estimated by only one survey for each territory in areas where the birds were free to feed. Perhaps territories with more efficient arthropod gleaners had fewer arthropods because of the feeding activity of the sapsuckers, while less efficient birds had more uncaptured

arthropods remaining during surveys. More exhaustive examinations of abundance, including measurements of arthropod numbers in areas on a territory where sapsuckers are excluded from gleaned arthropods, may yield different results than my study.

Data from cavity occupation suggest that suitable cavity sites or the ability to construct new cavities may be limited because birds that reused old cavities had lower reproductive success. I found that sapsuckers using old cavities fledged fewer young than birds in new cavities. Old cavities may be infested with high levels of parasites and nestlings raised in these cavities may experience higher mortality as a result. During my study I observed parasites on chicks in both types of nests but I was not able to quantify parasite levels. Future research could easily address this question about differences between new and reused cavities by examining parasite levels in the material at the bottom of the nest cavities as well as on the nestlings themselves. In addition, I also found that sapsuckers reusing old cavities laid more eggs than those in new cavities. Although this phenomenon could have several explanations, perhaps birds that are forced to use old nests lay more eggs to compensate for their anticipated greater chick loss in old, parasite-ridden nests.

Another indication that cavity sites or the ability to make cavities may be limited is that birds that started many cavities had later hatching dates than those that made only one or two cavity starts before obtaining a completed nesting cavity. Although this delay in hatching did not appear to translate into a delay in fledging for these territories, the sample size may be too small to detect significant differences at later nest stages.

I could not detect any significant differences between sapsuckers breeding for a second time and those known to be making their first breeding attempt. Sample size is low for these data but trends are not in the expected direction because new breeders actually fledged slightly more young at an earlier date on average than old breeders. Missing from these data is the age distribution of floater birds unable to breed because of a lack of suitable sites as well as the status of most of the mates of these marked birds. Perhaps most young birds are unable to obtain an opportunity to breed in their first year and those that do, are able to

pair with older established birds that have lost a mate. Thus, my comparison of 'experienced' and 'new' breeders may be complicated by missing information on mates and non-breeders.

I found evidence that birds in nest cavities were more frequently attacked by predators than adult birds away from their nests. This suggests that predation on cavities is more likely to limit sapsucker breeding success than loss of care-giving adults in this population. Explorations of factors affecting predator attack on cavities are needed. It is interesting to note that all successful predation on adult birds that I observed was on males. The reason for this pattern could be two-fold. Males have more red plumage and would be more conspicuous to color-sighted predators outside the cavity. And in addition, as is typical for all woodpeckers (Short 1982), males spend more time in the nest cavities than females, including staying in the cavities with the nestlings at night. Thus, males may incur a greater cost than females for this part of parental care because of the risk of predation in nest cavities.

I found variation in both the number of eggs laid and the number of successfully fledged young, although variation was higher for the number of fledglings. Reproductive success for yellow-bellied sapsuckers may be influenced more strongly by factors affecting the fate of offspring between egg stage and fledging than by factors that influence the number of eggs laid. Brood reduction was probably a combination of infertile eggs and nestling loss. Some nestling loss definitely occurred between the time the nestlings were eight days old and fledging. Nestling loss is unlikely to be a result of nestlings falling out of the deep cavity themselves because woodpecker chicks generally do not climb to the cavity entrance until a week before fledging (Jackson 1976). I conclude that chick loss was a result of some cause other than predation such as starvation, parasites, or removal from the nest by adults because 1) I never saw evidence of predator attack in most nests with brood reduction and 2) when predators attacked the nest they took all of the chicks. I never found whole dead chicks in a nest cavity and I could not determine exactly how brood reduction

occurred. Sapsuckers keep their nests clean by frequent removal of fecal material (Kilham 1962b) and it seems likely that dead chicks were removed to prevent fouling of the nest cavity.

I found no differences in breeding success between the three years of my study. Therefore, the variations in reproductive success that I detected in my study were likely a result of variation between individual territories in resource quality or the ability of the breeding adults to obtain those resources. According to my data, the most likely factor limiting the reproductive success of sapsuckers in this area is availability of nesting sites. Thus, the strongest selective pressures acting on individual sapsuckers may be in the ability to identify potential nesting trees, construct nests, and defend nest sites from other sapsuckers. However, my data for reproductive success are plagued by small sample sizes and incomplete data, making final conclusions difficult. My results from previous chapters suggest that sapsuckers have many unusual adaptations for extracting sap from trees and further research may reveal that the ability to obtain sap also has experienced strong selection in this unusual woodpecker.

## CHAPTER 7:

### DRUMMING IN YELLOW-BELLIED SAPSUCKERS: TESTING THE ENVIRONMENTAL ADVERTISEMENT HYPOTHESIS

#### Introduction

Drumming is a loud, rhythmic series of sounds produced when a woodpecker hammers its bill in split-second repetitions against a resonating object. Drumming is never produced when the substrate is being altered for feeding or nest building and is thus defined as a signal or display behavior (Lawrence 1967). Among acoustic displays, drumming is unusual because a separate instrument is required to produce the sound in addition to the bird's body parts (Skutch 1985). Based on this unusual use of an instrument, Winkler and Short (1978) proposed an environmental advertisement function for drumming. They suggested that drumming could contain valuable information about habitat quality if sound quality varies with the substrate that is used for the display. Thus, the environmental advertisement hypothesis (EAH) suggests that potential mates could use information contained in the sound of the drum to assess environmental quality and make territory settlement choices. Acoustic display often functions in both mate attraction and territorial defense but the EAH applies only to the mate attraction aspect of communication systems.

Although the EAH was originally proposed to explain drumming in woodpeckers, it could apply to other acoustic displays across a diverse array of organisms. Male Ruffed Grouse beat their wings together atop stumps and logs that may amplify their drumming display (Schemnitz 1976, Palmer 1963). Male lycosid spiders vibrate parts of their bodies against dry leaves to make and amplify an airborne acoustic signal (Harrison 1969, Rovner 1975, Stratton and Uetz 1981, Kohler and Tembrock 1987). Several species of kangaroo rats drum against the ground with their feet to produce airborne sound (Kenagy 1976,



Randall and Stevens 1987, Randall 1989). These airborne sounds are used in the context of mating and could transmit information about environmental quality to potential mates such as soil type for rats or water content or size of leaves for spiders. In addition to these airborne sounds, the seismic vibrations that are produced by many animals in soil, vegetation and water have the potential to convey information about the environment by the way these vibrations are transmitted. Further, the EAH has broader applications to the more typical acoustic displays that organisms make with their own bodies such as bird song, insect stridulation or amphibian trills. All airborne sounds are altered by environmental factors such as vegetation, humidity, temperature, and wind (Aylor 1972, Morton 1975, Linskens, et.al. 1976, Marten and Marler 1977, Wiley and Richards 1978, Henwood and Fabrick 1979, Richards and Wiley 1980, Waser and Brown 1986). By choosing specific sites for acoustic display, organisms may be able to advertise locations of high quality if the sounds that they produce are altered by the environment in particular ways. In this paper I will focus on the EAH as it applies to woodpeckers, the taxon for which it was first proposed.

The EAH predicts that woodpeckers will choose to drum on substrates that advertise the quality of their location. A high-quality territory for a woodpecker includes wood that is valuable for constructing nest holes, feeding or roosting. Most species of woodpeckers use dead wood for both feeding, nesting, and roosting. Several studies have shown the importance of keeping dead wood standing in a forest to maintain healthy woodpecker populations (Pettersen and Grubb 1983, Swallow et.al. 1986, Welch and Capen 1992). Dead wood, without the high water content of a living tree, would have a different sound than live wood. Thus, for the majority of woodpecker species, the EAH predicts that they will choose dead wood as a drum substrate.

A review of the drumming of woodpeckers of the world (Short 1982) shows that the majority of woodpeckers use dead wood for drumming, thus fitting the predictions of the EAH. A more in-depth study of Red-headed Woodpeckers (Melanerpes erythrocephalus)

(Venables and Collopy 1989) showed that this species preferred to drum specifically on the dead wood of a nest tree and not on other dead wood available, providing even stronger evidence for a possible environmental advertisement function. However, the problem with these trends is that they also fit an alternative explanation. In many environments, loud sounds at a low frequency have been shown to have better long distance transmission properties (Morton 1975, Marten and Marler 1978, Wiley and Richards 1978). Woodpeckers may take advantage of this phenomenon and choose drum substrates that produce especially loud and low frequency sounds. Thus the alternative to the EAH, the long-distance signal hypothesis (LDSH), predicts that woodpeckers should make the loudest and lowest sound possible with their drumming. The LDSH suggests that drumming in woodpeckers might be the functional equivalent of passerine bird song in a taxon with limited singing abilities (Gaunt and Gaunt 1985).

Given that the dead (and probably hollow) wood of nest trees that most woodpeckers use for drumming would also produce the loudest, lowest sounds possible in that environment, both the EAH and its alternative, the LDSH, have identical predictions, namely that woodpeckers will choose dead hollow wood for drumming either because this wood sounds like nest-tree wood or because it can be used to make long-distance sounds. How can the predictions of the EAH and LDSH be separated? A species of drumming woodpecker that does not use dead wood for feeding and nesting would provide the needed separation in predictions between the EAH and the LDSH. Yellow-bellied sapsuckers are just such a species.

Adult yellow-bellied sapsuckers feed on the phloem sap of live trees from shallow holes that they peck in the bark (Beal 1911, McAtee 1911, Kilham 1964, Tate 1973). Nestlings are fed a mixture of insects and sap. The insects are gleaned from the leaves and trunks of trees or caught in flight. Yellow-bellied sapsuckers rarely obtain food from excavations in dead, rotting wood as do many other woodpeckers. In addition, yellow-bellied sapsuckers make nesting cavities in live aspen that have been infected with a heart-rot fungus (Kilham

1962a, Lawrence 1967, Kilham 1977). Thus, dead wood is not used for nesting, roosting or feeding by yellow-bellied sapsuckers. Given these peculiarities, the EAH predicts that yellow-bellied sapsuckers should drum upon substrates that indicate the presence of a large quantity of live feeding and nesting trees. Thus, the preferred drum substrate predicted by the EAH is living wood. Conversely, the LDSH predicts that yellow-bellied sapsuckers should use a substrate that produces the loudest and lowest sounds possible.

## Methods

### Study Site and Observations

I observed yellow-bellied sapsuckers in 1991 and 1992 at the University of Michigan Biological Station in Cheboygan county. The habitat in this area consists of an 80 year-old mixed hardwood forest which grew up after extensive clear cutting of the original pine forest in the early 1900's.

Data on types of substrate used for drumming were collected from the time the first adults arrived from migration in early April until just after young were fledged from the nest in early July. Two sampling methods were used. Ad libitum observations of all drumming birds encountered were made in April and May 1991. Then in 1992, five individual sapsuckers were followed for up to four hours at a time and all drumming substrates of each focal individual were identified and marked. These focal-animal data were collected in April before the deciduous trees had developed new leaves which meant that long distance observations were possible through the branches in the forest canopy.

### Substrate Sound Quality Comparisons

Measurements of sound quality. Four aspects of the sound-producing potential of several types of substrate were measured. A comparison of the loudness of sounds that could be produced by drumming on different substrates was made with a knocking device. The knocking device consisted of a 5 cm diameter oak mallet mounted on a board with a screen-door spring which was attached at the end of the mallet's 24 cm handle. For each

knock on a substrate, the mallet was pulled back to a designated mark on the board and released 22 cm in front of a substrate. In combination with the spring, this system allowed knocks of equal force to be repeated on a variety of substrate. The amplitude of the resulting sounds of these controlled knocks was measured with a Realistic sound level meter also mounted on the apparatus at a fixed distance of 25 cm from the mallet's striking surface. Another device was used to measure three additional aspects of sound quality. This implement was made with a 15 cm long plastic crochet hook mounted perpendicular to one end of a small board (2 x 4 x 36 cm) and was also used to make hits against the different substrates. Strikes with the crochet hook device were recorded 30 cm away with an Audio-Technica AT815a directional microphone and a Sony Professional Walkman cassette tape recorder. Sound properties of these strikes that I measured included frequency in hertz of the longest lasting frequency component in the recording, length in seconds of the longest lasting frequency component, and frequency in hertz of the sound component with the greatest power (loudest). A UNISCAN sound analyzer was used to make these measurements.

Substrates tested. To show whether the drum substrates had similar sound qualities to food or nest substrates as the EAH predicts, the sound-producing potential of nest and food substrates were compared with all accessible drum substrates located in 1991. Nest substrates were defined as sites on trees 5-10cm above or below active nest-cavity entrances. A site on a tree that had 100 or more sap holes with some newly made wounds was defined as food substrate.

To see if a sapsucker chose a substrate with unique sound properties for drumming within a particular locale, I made controlled knocks and hits on substrates chosen for drumming and those not chosen. The sound quality measurements made from drum substrates were compared to averages of the sound quality measurements from the five closest neighboring trees to each drum substrate. I made the controlled knocks and hits on neighboring trees at the same height and in the same orientation as the matched drum

substrate. Furthermore, within the same branch or tree trunk, I compared the sounds of the specific site used for drumming to sites 20cm above, below, and to the side, for each drum substrate. Specific drum sites were easy to locate because sapsuckers leave small indentations in the wood during drumming from the force of their blows.

Statistical Analyses. I used a principal components analysis to explore the variation in sound quality from trees used for drumming, feeding, and nesting and to compare drum substrate with neighboring trees. A PCA of the correlation matrix of different sound qualities was conducted on the set of controlled-hit data regardless of substrate type. The PCA and component correlations ( $r$ ) were calculated using SAS JMP 2.0.4 computer software (SAS Institute 1991). I identified variables with significant component coefficients ( $P < 0.01$ ) for the drum, nest, and food substrate comparison and for the drum and neighbor comparison as having an important influence on the variation in PCA scores. A Kruskal-Wallis test was used to compare the scores of drum, nest, and food trees and a Wilcoxon matched-pairs signed-ranks test was used for the paired data of drum trees and neighboring trees (Hollander and Wolfe 1973). I compared the amplitude of the sound produced by controlled hits on drum substrates and on substrates within 20cm of the drum site on the same tree with a paired t-test.

#### Advertisement of Substrate Quantity

Sapsuckers may advertise the quantity of available sites as well as their quality. If sapsuckers are advertising quantity then they must drum on as many good substrates as possible that are available on a territory. To advertise the quantity they should also use drumming sites evenly. A 'good' substrate must indicate the presence of a nesting or feeding site. The alternative prediction is that sapsuckers will drum on only a select few of the substrates available presumably because of a particular substrate's position in the territory or because the sound that can be made from a favorite substrate is better than any other.

I identified 'good' substrates for this analysis as nest and food trees. I explored the possibility that nest or food trees differ structurally from other trees in the area. I surveyed the number of dead branches greater than 5cm in diameter on trees used for nesting and feeding and on a random sample of similarly sized forest trees. A Kruskal-Wallis test identified significant differences in branch number among the types of trees. Any unique structural properties of food or nest trees were then considered as possible features that sapsuckers could use to advertise the quantity of good substrates with their drumming.

To test whether sapsuckers advertised the quantity of good substrates available in an area, I observed all the substrates used for drumming by each of four individuals. I followed each individual for a total of 4-8 h during morning hours and noted how often sapsuckers drummed on each drum site. A drum site was defined as the specific location on a substrate where a bird made its drumming bouts. I counted the number of drum rolls made at each site. A drum roll was defined as a series of rapid taps followed by a pause that was longer than any of the intervals between individual taps. I defined a drumming bout as a series of drum rolls made continually on the same drum site.

I used Chi-square tests to determine if the number of drum rolls was evenly distributed among all the drum sites used by each individual. An even distribution was predicted for advertisement of the quantity of high-quality substrates available and uneven distribution favoring louder sites was predicted by the LDSH.

## Results

### Substrate Used for Drumming

Yellow-bellied sapsuckers never drummed at feeding or nesting sites (0/142 drumming bouts). Non-living substrate was used in 100% of the drum bouts that I observed while the majority (32/40) of individuals that I watched nested in live trees and all individuals used sap extracted from living trees as a source of food. Out of 142 bouts of drumming observed from 23 individuals, the preferred drum substrate (81% of bouts observed) was a

dead aspen branch still attached to the living tree. Also frequented were the old skeletons of huge 80 year old stumps (8%) and the dead wood of other species of trees (7%). A few birds drummed on human-made substrates including telephone poles, chimneys of cabins and an upturned metal boat (4%).

Table 7-1. Results of a principal component analysis of variation of sound quality of controlled knocks and hits on drum, nest, and food substrates.

	Component <sup>1</sup>					
	1		2		3	
	e	r	e	r	e	r
Measure of sound quality						
AMPLITUDE (dB)	0.61	0.93	0.24	0.22	-0.05	-0.38
FREQ. LLF <sup>2</sup> (hz)	-0.40	-0.61	0.60	0.55	-0.68	-0.56
TIME LLF <sup>3</sup> (min)	0.52	0.80	0.59	0.54	0.12	0.10
FPP <sup>4</sup> (hz)	-0.44	-0.66	0.49	0.45	0.72	0.59
Eigen value	2.315		0.853		0.675	
Proportion	0.579		0.213		0.169	
Cumulative proportion	0.579		0.792		0.961	

<sup>1</sup>Data for each of the first three principal components are loadings (e), component correlations (r), eigenvalues of correlation matrix, and proportion of the variance explained by each component.

<sup>2</sup>Freq.LLF=frequency of the longest lasting frequency

<sup>3</sup>Time LLF=duration of the longest lasting frequency

<sup>4</sup>FPP=frequency at peak acoustic power of the sound.

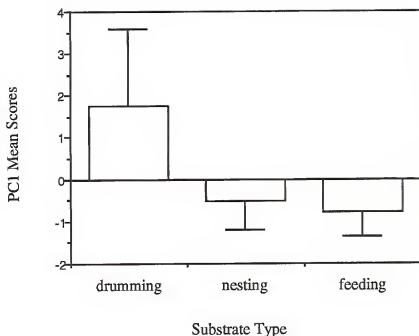


Figure 7-1. Mean ( $\pm$ s.d.) PCI scores for drum, food, and nest substrates.

#### Sound Quality Comparisons

The principal components analysis used to address the question of whether sapsuckers chose drum substrates with similar sound properties to nest and food substrates showed that the first principal component explained 58% of the total variation in sound quality of controlled hits. The first principal component (PC1) included all four of the sound qualities measured. PC1 scores correlated positively with sound amplitude and duration and negatively with the frequencies of both the longest and the loudest part of the sound of the controlled hits (Table 7-1). I found a significant effect of substrate type on scores of the first principal component (Kruskal-Wallis,  $H=22.864$ ,  $df=2$ ,  $P=0.0001$ ). The substrate used for drumming had different sound qualities than nest or food trees, but nest and food substrate did not differ in their acoustic properties from one another (Fig. 7-1). In



summary, drum substrates had louder, lower sounds that lasted longer than the sound produced on the nesting and feeding substrates (Table 7-2).

Table 7-2. Means ( $\pm$ s.d.) of the acoustic properties of controlled knocks and hits of drum, nest, and food substrates.

MEASURE OF SOUND QUALITY <sup>1</sup>					
SUBSTRATE					
	N	AMPLITUDE (dB)	FREQ. LLF (hz)	TIME LLF (min)	FPP (hz)
drum	13	89.09 $\pm$ 7.03	476.92 $\pm$ 103.87	0.145 $\pm$ 0.109	486.15 $\pm$ 227.94
nest	17	79.49 $\pm$ 1.01	540.00 $\pm$ 74.83	0.071 $\pm$ 0.022	745.88 $\pm$ 297.30
food	18	79.45 $\pm$ 1.10	588.89 $\pm$ 98.75	0.046 $\pm$ 0.014	671.11 $\pm$ 181.27

<sup>1</sup>see Table 7-1 for acronyms

The principal component analysis of the sound-producing qualities of drum substrates and similar substrates on neighboring trees revealed that 67% of the variation in the acoustic measurements was summarized in the first principal component. PC1 contained significant proportions of all four of the sound qualities. I found a positive correlation between PC1 scores and both amplitude and time. The two measures of frequency were correlated negatively with the scores of the first principal component (Table 7-3). I found that drum spots differed from similar locations on neighboring trees in the scores of the first principal component (Wilcoxon matched-pairs signed-ranks test,  $P=0.0015$ ,  $N=13$ ) (Fig. 7-2). In short, each drum substrate had lower, louder, and longer lasting sounds than matched substrates on its five closest neighbor trees (Table 7-4).

In a comparison of the sounds of drum substrates with the sounds of three nearby locations on the same tree or stump, I found that specific drum spots produced louder sounds than the wood surrounding them. (Wilcoxon matched-pairs signed-ranks test,  $p=0.0013$ ,  $N=15$ ) (Fig. 7-3).

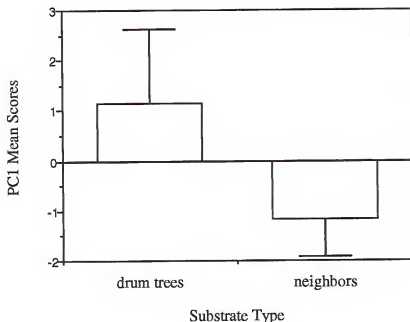


Figure 7-2. Mean ( $\pm$ s.d.) PCI scores for drum trees and neighboring trees not used for drumming.

#### Advertisement of Substrate Quantity

As noted above, sapsuckers preferred to drum on the dead stubs of live trees. A comparison of the number of dead branches per tree between nest and food trees and a random sample of similarly sized trees revealed that nest trees had an average of 4.73 dead branches per tree more than food trees or a random sample of trees (Kruskal-Wallis,  $H=36.089$ ,  $df=2$ ,  $p=0.0001$  Fig. 7-4). Thus, sapsuckers could indicate the quantity of dead branches present in their environment by using all substrates evenly and this information would translate into the quantity of nest sites available. However, continuous observations of five individual sapsuckers showed uneven distributions in the use of substrates (Fig. 7-5). The number of drum rolls given at each drum site was highly uneven (male A,  $X^2=213$ ,  $df=3$ ,  $p<0.001$ ; male B,  $X^2=32$ ,  $df=2$ ,  $p<0.001$ ; male C,  $X^2=81$ ,  $df=7$ ,  $p<0.001$ ; male D,  $X^2=26$ ,  $df=2$ ,  $p<0.001$ ). Each individual strongly favored one or two particular drum

substrates, directing as much 90% of their rolls to one tree while other substrates were used less than 1% of the time .

### Discussion

The EAH predicted that sapsuckers would drum on nesting or feeding sites or both. Because I never observed sapsuckers drum on the trunk of a nesting or feeding tree, this first prediction can be rejected. Further, sapsuckers do not choose drum substrate that has sounds that are typical of feeding or nesting substrate. Thus, I conclude that sapsuckers do not advertise the quality of particular nesting or feeding spots with their drumming.

Table 7-3. Results of a principal components analysis of variation of sound quality of controlled knocks and hits between two different types of substrate, drum sites and their neighboring trees.

	Component <sup>1</sup>					
	1		2		3	
	e	r	e	r	e	r
measure of sound quality						
AMPLITUDE (dB)	0.57	0.93	0.28	0.24	-0.09	-0.06
FREQ. LLF (hz)	-0.49	-0.80	0.41	0.35	0.71	0.48
TIME LLF (min)	0.49	0.80	0.63	0.54	0.20	0.14
FPP (hz)	-0.45	-0.74	0.60	0.51	-0.66	-0.44
Eigen value	2.696		0.730		0.448	
Proportion	0.674		0.182		0.112	
Cumulative proportion	0.674		0.856		0.968	

<sup>1</sup>abbreviations same as in Table 7-1.

Table 7-4. Summary of the mean ( $\pm$ s.d.) acoustic properties of drum substrate and neighboring trees.

SUBSTRATE	N	MEASURE OF SOUND QUALITY <sup>1</sup>			
		AMPLITUDE (dB)	FREQ. LLF (hz)	TIME LLF (min)	FPP (hz)
drum site	13	88.76 $\pm$ 6.79	505.7 $\pm$ 225.5	0.137 $\pm$ 0.108	476.9 $\pm$ 95.9
neighboring trees	13	79.63 $\pm$ 1.22	795.5 $\pm$ 204.8	0.059 $\pm$ 0.016	664.3 $\pm$ 157.9

<sup>1</sup>see Table 7-1 for acronym

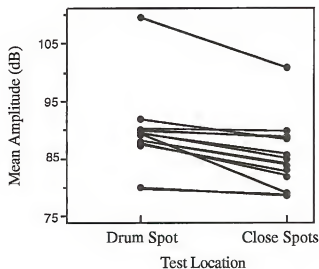


Figure 7-3. A comparison between the mean amplitude of sounds of controlled knocks (defined in text) on locations chosen for drumming and the nearby wood surrounding each location.

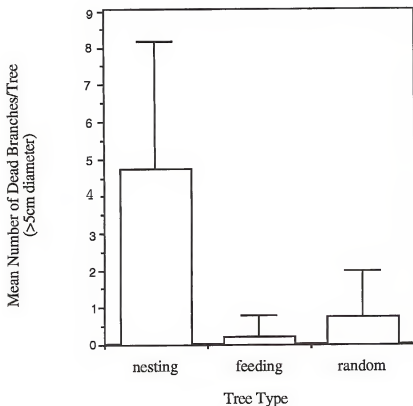


Figure 7-4. Mean ( $\pm$ s.d.) number of dead branches (> 5 cm diameter) in nest trees, trees used for feeding, and a random sample of similar sized forest trees

I found that sapsuckers drum on the dead branches of living trees more frequently than on all other types of substrate. Because nesting trees have more dead branches than other trees, sapsuckers might advertise the presence of nesting sites by demonstrating the presence of a large quantity of dead branches. However, I found no evidence that the pattern of drumming advertises the quantity of substrate present which is the only way that drumming on dead wood would indicate a potential nest site in this species. The numbers of drum rolls given on different drum substrates showed a highly skewed distribution with most drumming directed to one or two drum sites. Thus, based on my overall observations, the EAH for woodpecker drumming can be rejected for yellow-bellied sapsuckers in favor of the alternative LDSH.

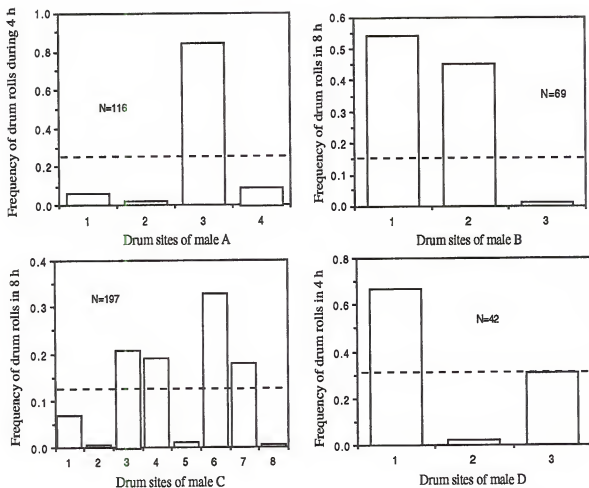


Figure 7-5. A comparison of drum site preferences for four male yellow-bellied sapsuckers observed continuously for 4-8 h. Bars on graphs show observed numbers of drum rolls per site and horizontal lines represent the expected number assuming an even distribution of use. Total number of drum rolls observed for each individual is noted on each graph.

I have rejected a hypothesis about mate attraction, the EAH, in favor of an hypothesis that can apply to both the mate attraction and territorial defense functions of acoustic display, the LDSH. This is a fair test in sapsuckers because they use drumming during pair formation (pers. obs.) and drumming is probably involved in mate attraction. However, if drumming functions strictly as a territorial defense display for other woodpeckers then the LDSH is the only hypothesis expected to fit their acoustic display. More information about the context of drumming is needed before the EAH can be tested for all woodpeckers.

Drumming in woodpeckers offers a unique opportunity to study acoustic display as an advertisement. Normally, when only an organism's own body is involved in sound production, it is impractical or impossible to define the range of sounds that the organism is capable of making. Such a question involves difficult long-term study, invasive manipulations, or studies of captive animals. In species that use substrates, however, one can measure the sound-producing properties of the substrate used to make the display and a range of possible sounds can be identified. Knowing the sound-producing capabilities of an organism helps in understanding the function of advertisement because the sounds it chooses to make when performing a particular acoustic display can reveal how far and therefore to whom that display is directed. For example, I have shown that yellow-bellied sapsuckers make sounds on substrates that produce the loudest and lowest sounds possible in an area. This suggests that they are covering the greatest possible range with their type of acoustic display. In conclusion, drumming by sapsuckers does not have the unusual function of advertising the environment as first hypothesized by Winkler and Short (1978) for woodpeckers, but drumming is a unique signal among birds which allows an analysis of sound that is not easily possible for song.

## SUMMARY AND CONCLUSIONS

Yellow-bellied sapsuckers have a variety of adaptations to exploit both xylem and phloem sap for food. Plants protect their sap with defensive mechanisms. I found that sapsuckers may be able to overcome these by concentrating their efforts on individual trees, repeatedly wounding in vertical lines of sap holes, and possibly using saliva to unblock clogged sap tissue. In addition, an examination of reproductive success revealed that sapsuckers may be limited by the availability of nesting sites. My experiments with their drumming substrate indicated that sapsuckers use drumming as a long-distance signal probably for territorial advertisement. In the following sections, I will discuss the implications of each of these findings and explore the possible evolution of these adaptations.

### Sap Feeding

During a brief period in early spring, yellow-bellied sapsuckers extracted xylem sap for food. Xylem sap flowed freely from holes made through the bark into the wood of trees at this time and I obtained fresh sap easily from trees with my own artificial holes. This offered a unique opportunity to examine the quality and quantity of sap in preferred trees. The ease of xylem sap extraction could be exploited for future research on sap-feeding organisms. The fact that xylem sap flowed copiously from my incisions suggests that no specialized adaptations are needed to extract xylem sap in early spring other than the ability to incise bark.

Sapsuckers left a characteristic pattern of single holes and short lines of horizontal holes after feeding on xylem sap in my study area. This pattern is reminiscent of the types of holes sapsuckers make during migration and on their wintering grounds (Tate 1973,



McAtee 1911). It is possible that during most of the year, sapsuckers exploit xylem sap rather than phloem sap. Other species of woodpeckers have also been observed to feed on tree sap from horizontal bands of holes (Turček 1954, Gibbs 1983, Ullman 1985). Although little is known about the sap they collect from these holes, with my evidence from sapsuckers, I suggest that these other species are also exploiting xylem sap from trees. Future research should examine whether these birds are actually feeding on dilute xylem sap and how important such sap is in their diet.

In contrast to xylem sap, phloem sap did not flow freely from my artificial incisions during the time sapsuckers exploited this sap as food. I found evidence for at least three specialized adaptations for extracting phloem sap in this species. 1) Sapsuckers chose specific trees for sap extraction. Individual trees may be more desirable because of increased solutes in their sap, including sucrose and amino acids but more research is needed to confirm this. 2) Sapsuckers appear to obtain more sap than otherwise possible by repeated wounding of a single tree. 3) Sapsuckers may also be able to stimulate the flow of sap with the use of saliva. Thus, a combination of adaptations probably allows for the successful exploitation of phloem sap for food.

With this information on feeding habits, a picture begins to emerge of the evolution of sap feeding in woodpeckers. Although evidence is scanty, more species appear to exploit xylem sap than phloem sap (Gibbs 1983). My research suggests that the only specialization needed for xylem sap extraction is getting through the bark, an adaptation that woodpeckers already possess. Thus, it is not surprising that many woodpecker species feed on xylem sap. However, because many specializations are needed for phloem sap extraction, only a few woodpeckers are able to exploit this resource. To date, the only three species of phloem extractors that have been identified in this family are acorn woodpeckers (Kattan 1988), rufous-bellied woodpeckers (Zusi and Marshall 1970, Ripley 1989), and North American sapsuckers (Tate 1973, this study). Perhaps xylem feeding is a prerequisite for the development of a more specialized phloem-feeding habit. Future

research should examine whether acorn woodpeckers and rufus-bellied woodpeckers also exploit xylem sap and what specializations these two species have for phloem-sap extraction.

### Reproduction and Territoriality

I found evidence that the ability to obtain good nesting sites may limit reproductive success in yellow-bellied sapsuckers. I did not find the same trends for the availability of sap feeding sites or arthropods. However, I may have been unable to detect whether food was a limiting resource because sample sizes in this part of my study were small and many characteristics of food availability such as the total sap flow on a territory were not measured.

Sapsuckers use drumming in long-distance territorial advertisement. In particular they drum at the end of the breeding season when they no longer need nesting cavities but they still have active sap wells where fledglings and parents feed. This suggests that access to sap wells, and not cavities, is the benefit that makes the cost of territoriality worthwhile. Perhaps because each sap well requires a large investment of time and energy to induce sap flow through repeated wounding, sapsuckers gain more benefits by vigorously defending their current sap wells rather than attempting to start new wells. Future research will probably reveal that the ability to garner large quantities of high-quality sap also increases reproductive success.

### Possible Evolutionary History of Sapsucking in Sapsuckers

Sapsuckers are strictly North and Central American in distribution (Howell 1952). Because all species in the genus Sphyrapicus extract phloem sap for food (Ehrlich et al. 1988), the specializations for this type of feeding habit probably evolved when this genus diverged from related forms. Evidence indicates that the most closely related genus to Sphyrapicus is Melanerpes (Short 1982, Tennant 1991) although some have suggested that

the genus Picoides may be more closely related (Swierczewski and Raikow 1981). All three of these genera have been observed to feed on xylem sap (Tate 1973, Gibbs 1983). What forces led to the evolution of the additional adaptations needed to exploit phloem sap? At least four genera of woodpeckers overlap the range of Sphyrapicus in northern North America (Ehrlich et al. 1988). All of these woodpeckers exploit arthropods for food and many species compete for access to arthropods, especially in times of low food availability (Willson 1971, Wallace 1974, Conner 1981). Perhaps competition for food resources during times of low arthropod abundance served as a selective pressure favoring the evolution of phloem feeding. Such a novel food resource may have allowed sapsuckers to coexist with other species of woodpeckers in areas where competitive exclusion would have otherwise eliminated sapsuckers.

Sapsuckers favor early-successional species of trees for both nesting (aspen) and feeding (white birch and red maple). While populations of other species of woodpeckers may be influenced by the availability of dead snags of any tree species for nesting and feeding, sapsuckers have very specific requirements. Another group of woodpeckers that has similar specific habitat requirements is the three-toed woodpeckers (Ehrlich et al. 1988). These woodpeckers show rapid changes in population size in a given area dependent on habitat availability (Yunick 1985). Thus, sapsuckers, with their requirements of early-successional trees, may also experience large changes in populations as habitats change.

Sapsuckers were one of the most abundant woodpeckers in Northern Michigan. This area is characterized by a relatively young forest of early-successional trees which grew up after extensive logging. The pre-settlement virgin forest was characterized by a more patchy distribution of early-successional species because these species would only become established in tree fall gaps, after forest fires, and after major wind storms (Foster 1988). Sapsuckers may have been less common in the pre-settlement forest and limitations of nesting and feeding trees may have been more severe than they are today.

Reconstructions of Holocene vegetation histories of northern North America show that species such as white birch and aspen dominated the first forests after deglaciation (Garralla and Gajewski 1992, Bennett 1992). Because of the specific requirements that sapsuckers have for these colonizing species, populations of sapsuckers may have been very large during periods in the past, corresponding to periods of glacial decrease. The colonization of these new forests, coupled with competition with other woodpeckers for arthropods, could also have favored the evolution of sap feeding in sapsuckers.

Finally, as noted in the introduction, sapsuckers serve as keystone species in their community by providing a valuable food resource to many species of organisms. Miller and Nero (1983) suggest that hummingbirds have an extended range because of their association with sapsuckers. An examination of the evolution of these associated species would be an excellent way to explore trends in sapsucker evolution. In addition, research on why so many species steal sap from sapsuckers rather than extract it themselves may reveal additional insights on how and why sapsuckers obtain phloem sap for food.

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## BIOGRAPHICAL SKETCH

Laurie Eberhardt was born January 25, 1963, in Angola, Indiana. Her interest in biology began early, instigated by parents who were very active in local land conservation programs. She went to public school through high school in Angola, Indiana, then moved to Richmond, Indiana, to attend Earlham College. She was greatly influenced by the excellent biology program at Earlham and was active in the campus natural history museum both as a curator and museum guide. During her senior year, she participated in a biology and sociology term abroad in Kenya, East Africa. After graduating in 1985, she returned to Kenya to assist in a field study of babblers. Before starting graduate school at the University of Florida, she worked at a University of Wisconsin field station on a study of freshwater snail assemblages in northern Wisconsin and at a water quality testing laboratory in Indiana. She received a Master of Science degree from the University of Florida in 1990 for her work on oxygen consumption during singing in male Carolina Wrens. Her research on yellow-bellied sapsuckers allowed her to return to favorite old haunts in the upper Midwest. After completing her PhD she will take a position as an assistant professor in the biology department at Valparaiso University. She hopes to involve undergraduates in her work as she continues research on sap feeding and sapsuckers.



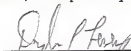
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Professor of Zoology


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Professor of Zoology

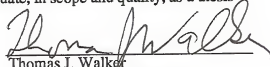
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Douglas J. Levey  
Associate Professor of Zoology

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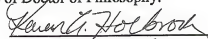
  
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This thesis was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1994

  
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